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A Textbook of
SYSTEMATIC BOTANY

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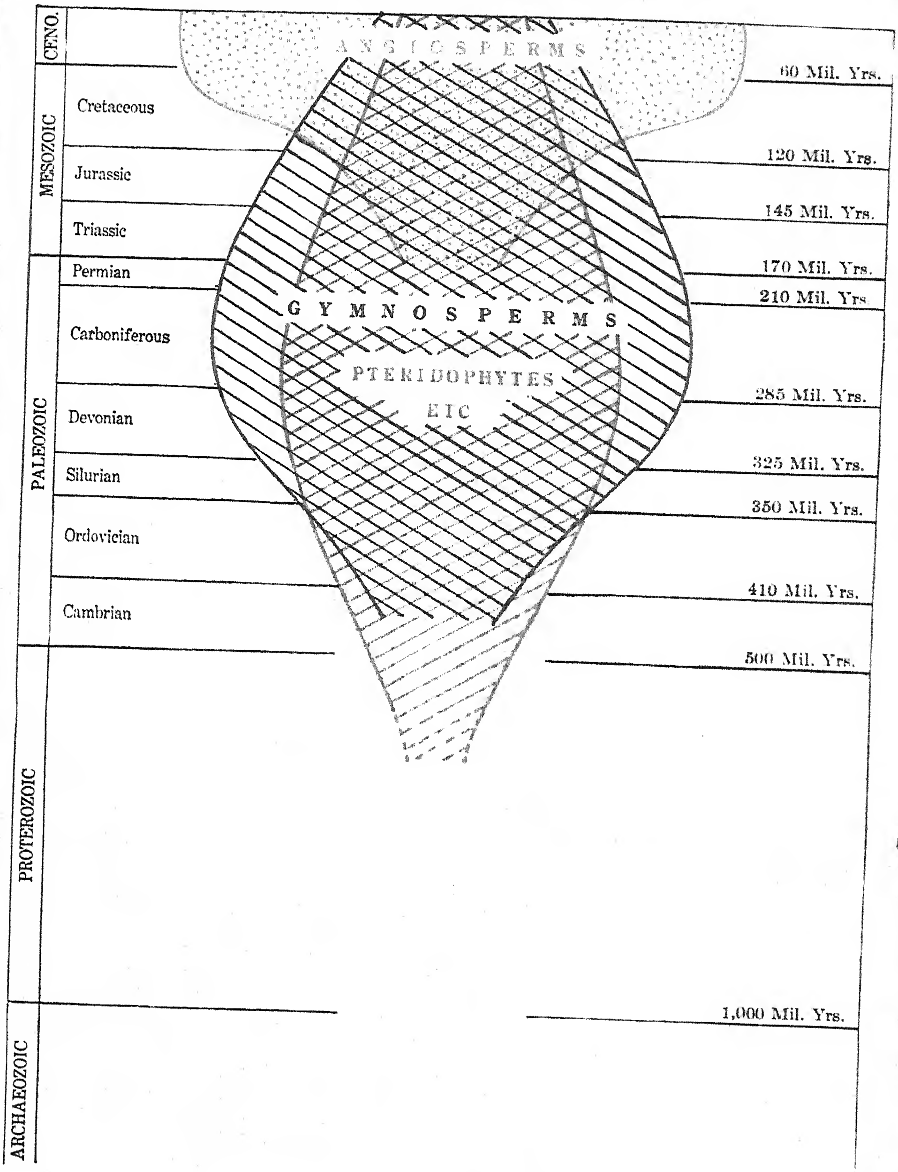
DEVELOPMENT OF PLANT LIFE



FRONTISPIECE.—Successions of plants, showing the estimated time of origin of the different groups and the relative prevalence at different periods. (*Modified after Berry.*)

A TEXTBOOK OF
Systematic Botany

by DEANE B. SWINGLE, *Ph.D.*
Late Professor of Botany and
Dean of the Division of Science
Montana State College

Third Edition
Third Impression

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A TEXTBOOK OF SYSTEMATIC BOTANY

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TO MY WIFE
WHO HAS BEEN MORE
TO THIS BOOK
THAN COAUTHOR

PREFACE TO THE THIRD EDITION

When the first edition of this book was published in 1928, it was the only work in which the principles and procedures of taxonomic botany had been assembled in textbook form for classroom use. Prior to that time students in this field had learned to name plants mostly by the apprentice system, sometimes supplemented by informal—rarely by formal—lectures. The situation was aptly stated by A. S. Hitchcock, himself a teacher for many years, in his "Descriptive Systematic Botany" published in 1925. "Descriptive taxonomy at present may be likened to a craft, in which the art or technique has not been committed to writing but is handed down by tradition." Again in the text he states, "The student's first experience in the general identification of plants may be obtained while he is serving as an assistant in botany at a college or an experiment station."

Since that time, the situation has radically changed. Students in systematic botany have always wanted a textbook in this field, and belatedly teachers of the subject are becoming "textbook-minded." They now realize that even good formal lectures need to be supplemented by a textbook here as in other branches of science, and that fragmentary assignments to technical literature do not serve the same purpose to beginners.

This third revision has involved two major problems: (1) the sequence in which the topics should be presented, and (2) the determination of what should be presented in an introductory course and what should be reserved for advanced work.

As for the sequence of chapters, the principal change in this revision has been to introduce the actual study of plant groups earlier, deferring the more abstract principles until later in the course. However, the subject matter is so organized that, after the first two chapters have been studied, the others can be taken up in almost any sequence.

The choice of material to be included in the book is more difficult, and some things are included that most beginning students will not use. This statement applies especially to the reports of recent taxonomic researches and to references to books that undergraduates have little occasion to consult. However, there is little demand for a textbook of advanced taxonomy, so it

seems best to include some of these references here, to be referred to in later courses.

Teachers of plant taxonomy have not yet settled down to anything approaching a standard method of introducing this subject to the students. Probably there is more difference here in the method of approach than in any other branch of science. The author has made a special effort, through correspondence with many distinguished botanists, to produce a book that will satisfy the requirements of most teachers of taxonomy. The question of including the "experimental method" of geneticists and ecologists in an introductory book while that subject is so new and calls for advanced prerequisites is a difficult one. It has been solved by explaining the method and its accomplishments and limitations in an elementary way in appropriate places, particularly in Chaps. I, X, and XII, and leaving the further development of it for advanced courses.

Most of the chapters have been thoroughly revised and amplified, some almost entirely rewritten, and a new one has been added on methods of identification; but at the same time an effort has been made to keep down the size and cost of the book so that it will not be prohibitive for the student to buy both it and the necessary manual for the identification of his collection.

This opportunity is taken to express the author's gratitude for the help given in the revision by a number of taxonomists. Especial thanks are due to Dr. David D. Keck of the Carnegie Institution for his help in presenting the "experimental method," which lies in his field of research; Dr. George H. M. Lawrence of the Bailey Hortorium, Cornell University, for valuable suggestions on almost every chapter; Dr. Lincoln Constance and Dr. Willis L. Jepson of the University of California; Dr. Herbert F. Copeland of Sacramento, California Junior College; Dr. H. T. Darlington of Michigan State College; Dr. H. R. Totten of the University of North Carolina; Dr. J. M. Greenman and Dr. Edgar Anderson of the Missouri Botanical Garden; Dr. Aaron J. Sharp of the University of Tennessee; Dr. George Neville Jones of the University of Illinois; Dr. W. E. Booth, Montana State College; and Mrs. Lois Payson, librarian of Montana State College, for her indispensable help on the literature of systematic botany.

BOZEMAN, MONT.,
January, 1944.

DEANE B. SWINGLE.

PREFACE TO THE FIRST EDITION

It is a matter of more than passing interest that in the oldest branch of botany comparatively little attention has been given to methods of presentation to the student. While the teaching of most botanical subjects in our colleges is on a par with that of other branches of learning, the teaching of taxonomy, especially that of the higher plants, is not always a credit to the profession. Too often highly trained specialists, with a vital interest in their collections and an intense zeal for precise distinctions and accurate determinations, are content to lead their students through the paths of the apprentice, with little regard for anything but the technique of collecting, preserving, and naming, and certainly with little attempt to unfold to them in logical sequence the underlying principles of this branch of botanical science. Of late, a few teachers are giving lectures on the principles fundamental to systematic botany, but lectures not supplemented by assigned reading are wholly inadequate for the beginner. In the field of general botany we have a wealth of textbooks, some of them splendidly written; and in plant physiology, histology, ecology, and even in the newer fields of cytology and phytopathology a few good texts can be found. But while the naming and classifying of plants have been going on for centuries, no textbook is available that adequately sets forth the principles of taxonomy and nomenclature.[1]

A number of good reference books there are, to be sure, and many valuable papers on most phases of the subject. International congresses have been held to encourage uniformity in principle and practice. We have good systematists, and others are being reared to take their places. Notwithstanding these facts, however, no textbook is available to bring systematic

[1] The author has not overlooked two books of especial value in this connection. The first is J. C. Willis' "Flowering Plants and Ferns" which contains some valuable information on principles and methods. The second is A. S. Hitchcock's "Descriptive Systematic Botany" published in 1925. Professor Hitchcock's book is especially valuable in its up-to-date treatment and its well-chosen topics fundamental to modern taxonomy and nomenclature. From the preface and the method of treatment, however, it is evidently intended as a reference book rather than a classroom text.

botany to the student in logical and pedagogical form. It is for this reason only that these pages are written.

This book is an outgrowth of a course given at the Montana State College for the last fifteen years. It is designed to cover one semester, preferably the second, so that the fundamentals may be established during the colder months, and supplemented by field work with the opening of spring. Systematic botany should be preceded by a course in general botany, without which the student will fail to grasp the fundamental principles of phylogenetic taxonomy and will find that the examples used are mostly unfamiliar and meaningless.

It is not intended that this text shall in any way supplant the manuals used for identifying plants. These are already numerous and cover the flora of practically every part of the country, though lacking somewhat in harmony of detail, and this book is to supplement rather than to compete with them.

The purpose of the first part is to set forth and illustrate the principles and rules on which systematic botany is based. The second part describes some sixty families of spermatophytes, chosen because of their size, economic importance, or peculiar interest. To secure best results, a considerable portion of the time must be given to laboratory and field work, chiefly devoted to actual identification of the local flora by the use of the keys and manuals best suited to that locality.

The author takes this opportunity of expressing his gratitude to all who have aided in the work, either through valuable suggestions or the use of their libraries, and especially to R. A. Harper of Columbia University, J. E. Kirkwood of Montana State University, Ernst A. Bessey and H. T. Darlington of the Michigan Agricultural College, A. S. Hitchcock of the U. S. Department of Agriculture, M. L. Fernald of Harvard University, Aven Nelson of the University of Wyoming, Alfred Gundersen of the Brooklyn Botanic Garden, and R. J. Pool and T. J. Fitzpatrick of the University of Nebraska.

DEANE B. SWINGLE.

BOZEMAN, MONT.,
February, 1928.

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WHAT IS SYSTEMATIC BOTANY?

Systematic botany is the science of classifying and naming plants. Plant taxonomy lays emphasis on classification as an expression of phylogenetic relationships, and nomenclature provides each species with a name. Systematic botany includes both. Some people's interest in systematic botany is satisfied by a knowledge of the local flora and an ability to identify it, an interest that has been widened by automobile travel. This is but a limited aspect of a large subject. Important work in this field is the building of great herbaria with specimens from all over the world classified chiefly by comparative morphology. A newer taxonomic outlook is the study of the progress of evolution through experimental work, by crossing plants of different degrees of relationship, studying the products under different environmental conditions, and noting their establishment as new species or subspecies or their failure to survive for genetic or ecological reasons.

The modern systematic botanist, if he is to go far in his profession, needs a good background in general botany, cytology, genetics, ecology, plant geography, and paleobotany; otherwise, he can only collect, name, preserve, and catalogue plants, without understanding their origin. This is all the amateur systematists and some professionals attempt to do.

Obviously the students of systematic botany need to devote years of time to the subject, and teachers are much at variance as to the sequence in which the different topics should be presented. The trend, however, is toward having classes in the first course become familiar with as many plants as possible, know the principles involved, and receive an introduction to the newer experimental methods of geneticists and ecologists, which are not yet well enough established to be presented in dogmatic form.

Advanced courses in systematic botany should keep in close touch with research in all related fields.

A TEXTBOOK OF SYSTEMATIC BOTANY

INTRODUCTION

Modern systematic botany holds a unique position. It is in itself a science with its own ideals and its own rules and principles. The orderly classification of the wealth of vegetation that adorns the earth, a terminology understood by all nations, an application of the laws of evolution—these things in themselves are worthy of man's best efforts. It has, however, another service to perform. It must aid those in other fields of endeavor, who make use of plants for many purposes, to know the identity of the kinds they use and their relationships to others.

Nomenclature deals with names, which may or may not indicate relationships. Taxonomy seeks to group plants on a basis of similarities and differences, these being, as we now believe, expressions of actual phylogenetic relationships—"blood relationships" as we say of the higher animals. We might conceivably have names without classification, but we can scarcely have classification without names. Indeed, names are necessary in almost any kind of discussion.

Particularly close is the relationship between systematic botany and ecology. Names have little interest in themselves. It is only when attached to objects of study that names become significant. The out-of-door botanist not only names the plants but also notes their distribution, environment, seasonal development, and characters suggestive of economic value.

EARLY BOTANICAL WORK IN AMERICA

In America the development of botany in all its aspects has been an interesting one. The first distinguished American botanist was John Torrey, who, after graduating from the College of Physicians and Surgeons in New York, found greater interest in plants than in medicine and became New York State Botanist in

1836. He established two journals, the *Flora of the State of New York* and *Flora of North America*, and helped to start the young Asa Gray on his career in botany. The Torrey Botanical Club with its two publications, the *Journal of the Torrey Botanical Club* and the *Torrey Botanical Club Memoirs*, testifies to the great esteem in which he was held by the younger botanists of his time.

America's great pioneer systematic botanist, Asa Gray, after graduating in medicine and gaining an inspiration and much botanical knowledge from John Torrey, studied for a time with the more experienced botanists of England and returned to this country, where he was made Professor of Natural History at Harvard University, a position that he held up to the time of his death in 1888. He found in this country a veritable paradise, a vast and little-explored region with many familiar forms and not a few that were new to science. His tireless efforts, boundless enthusiasm, keen discrimination, and sympathetic attitude endeared him to his students and associates. It is little wonder that his modest laboratories became a Mecca for American botanists, both professional and amateur.

Gray's influence was far-reaching, especially as it came during a period when many were becoming interested in work on the flora of this new country. In colleges and universities the taxonomic aspect of botany became almost an obsession. The making of herbaria dominated botanical departments. Dr. Gray had sought to have centered at Harvard University a well-balanced series of courses in botany, including morphology and physiology, but the general enthusiasm ran irresistibly into the taxonomic field. As a result, many in the next generation of botanists used and taught this branch almost to the exclusion of others. This was quite unfortunate, for the impression was given that the chief purpose of botany was to collect and name plants. Indeed, in the minds of many people botany meant nothing else. Such an objective alone could hardly meet the approval of the masses, and botany lost favor accordingly. Appropriations were grudgingly given, and many students resented the courses where the practical value was not obvious. Fortunately, America produced a few great men who, in addition to being distinguished systematic botanists, had a broad outlook on the entire field of botany and were truly inspiring teachers. The strenuous efforts of Charles E. Bessey, W. A. Kellerman, W. G. Farlow,

John M. Coulter, and others soon restored the balance of emphasis in the colleges, and, indeed, the pendulum again swung too far. Many of the herbaria were stored away, classification ceased to be taught, and hundreds of students graduated from botanical courses without knowing the names of even a score of plants and without ever having attempted to use an analytical key. The layman, however, moving more slowly, continued to believe that botany had its beginning and end in nomenclature.

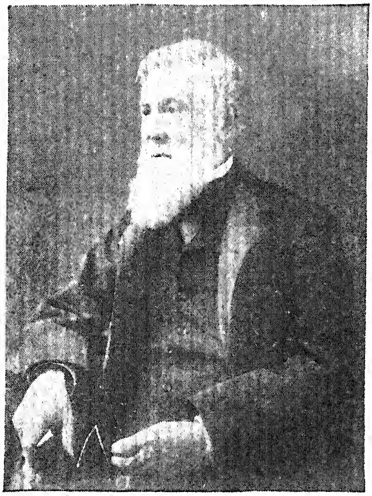


FIG. 1.—Asa Gray (1810–1899). Great pioneer systematist of Harvard University and inspiration to many American botanists. (*Courtesy of Alfred Gundersen, Brooklyn Botanic Garden.*)

FIG. 2.—John M. Coulter (1851–1928). Systematist and morphologist, and inspirational teacher. For 30 years head of the department of botany in the University of Chicago. He was highly instrumental in establishing botany in America on a broad basis. (*Courtesy of Alfred Gundersen, Brooklyn Botanic Garden.*)

Systematic botany in this country has now found its proper place with the other branches of botanical science. It has its highly trained specialists, most botanical students include it in their curricula, and the amateur finds in it his chief source of delight.

Fortunately, the antiquated methods of teaching systematic botany by the apprentice method are being replaced by the more modern ones using lectures, laboratory work, and field trips and grounding the student in the principles of taxonomy and the

rules of nomenclature that have made botanical science as a whole a subject of respect.

PURPOSES OF SYSTEMATIC BOTANY

The absolute dependence of man upon plants, the many kinds that he uses, and the varied purposes he finds for them have long made the necessity for plant names of some kind imperative. To primitive peoples, who were content to apply some kind of name to only those species that were especially useful, harmful, or interesting, and who traveled but little, relationships of species were rarely thought of. Just a few simple names served every purpose. However, the application of scientific thinking to considerations other than economic called for a more orderly procedure.

It should be clearly understood at the outset that the study of systematic botany involves two major procedures: (1) the establishing of the relationships that exist naturally between many groups of plants, and (2) the giving of names, common or scientific or both, to all groups or kinds of plants. The first is called *taxonomy* and the second *nomenclature*. The scientific mind is not content with names alone. If we study any group of objects, from atoms to heavenly bodies, we inevitably endeavor to classify the members of the group. This orderly arrangement is the first step in scientific treatment.

The systematic botanist finds about him millions of individual plants. No two are *exactly* alike, yet some are nearly so, while others are so different that they show scarcely any bond of relationship. By noting and comparing the similarities and differences, the makers of this science have brought out of chaos a fairly orderly system. Thus a profession has been set up in which the specialist, by establishing names and descriptions of thousands of specimens, performs a service to all who deal with plants. He determines their group relationships, their distribution, properties, and other points of interest. Systematic botany forms a groundwork for all sciences dealing with plants.

The myriad uses of plants make it necessary for many people who are not taxonomic specialists to have some knowledge of plant names and classifications. When we consider that green plants offer the greatest means of utilizing energy from the sun, that plants directly or indirectly furnish most of our food, cloth-

ing, shelter, fuel, medicine, paper, decorative materials, and many other useful things, we are made to realize that an orderly classification of them, understood in some measure by all civilized people, does much to prevent confusion and to facilitate cooperative effort.

Forestry.—Very extensive use of systematic botany is made in forestry. Every kind of tree must be named and classified, and its characteristics, distribution, and abundance must be learned. But forestry is not limited to the production of lumber. The national forests are extensively used for the grazing of livestock; and those who control the leasing and use of forest lands for this purpose must be familiar with all forms of vegetation and must know the palatability and food value of each kind, its methods of propagation, and the amount of grazing it will stand without danger of depletion. Furthermore, increasing use is made of the forests for recreational purposes, and national parks and forestry services are publishing splendid bulletins, some with beautiful illustrations, on the plants and shrubs that are most attractive to visitors.

Agriculture, Horticulture, and Floriculture.—In the broad field of plant breeding extensive progress has been made in recent years in the securing of improved varieties of grains, fruits, flowers, etc. This is not accomplished by haphazard tests but follows definite procedures. Crossing is usually involved, and a knowledge of species and varieties from a world standpoint is required to secure suitable stocks for the purpose. Even varieties resistant to diseases that can be controlled by no other method have been secured in this way. Foreign seed and plant introduction is done mostly by men well versed in systematic botany.

Range Management.—As the years go by, the American people are becoming more conscious of the fact that our once fertile lands, both wooded and prairie, are being exploited to a point where erosion and dust blowing, added to a depletion of humus and of inorganic food materials—especially nitrates, phosphates, and potash—by cropping have become national problems. Courses in range management are being established that make more study of plant life than of livestock. We are coming to realize that the conservation of native grasses and other plants and the selection of species best suited for holding the soil call for the efforts of ecologists who are well trained in systematic

botany. Indeed, forestry and range management furnish the greatest practical application of this branch of botanical science.

Ecology.—The character of the vegetation has long been known as a valuable index of soil conditions. Certain species are definitely hydrophytic, xerophytic, or halophytic, and soil characters of all kinds may be indicated by the vegetation growing on the surface. In many cases good ecologists can quickly interpret the character of a land area by its vegetation, with little or no study of the soil itself.

The plant ecologist must be a close student of systematic botany, knowing both the names of plants and their relationships, for his conclusions with regard to the effects of environment and the succession of species on an area would be wholly misleading if applied to species or groups different from the ones specified.

The helpfulness of systematic botany and ecology is mutual, for, as explained later, a wholly new conception of plant species and their evolutionary origin is coming from a combination of genetic and ecological studies made by crossing related plants and studying the resulting products.

Paleobotany.—One of our greatest difficulties in tracing relationships of plants and animals is that the ancestral forms connecting existing species have disappeared. The scattering fossils that are found here and there, though presenting a fragmentary picture, are very useful in revealing the characters of these ancestral forms and have real significance to those who have for a background a knowledge of taxonomy. Much of the research in taxonomy is concerned with piecing together the discoveries in paleontology, genetics, cytology, and other branches of science into a working plan of classification.

In many groups classification has proceeded only far enough to associate certain forms of life that have a kind of resemblance that may or may not represent actual relationship. The systematic botanist has not yet reached the place where he can afford to be static. His classification must be flexible and frequently revised to embody new information and to adjust itself to the newer viewpoints. If he takes this progressive attitude he can be of tremendous service in summarizing and utilizing the discoveries of investigators in related fields. He has a duty beyond the mere naming of plants.

From the foregoing it will be seen that collecting the flowering

plants of a limited region and learning their names is but a simple and superficial part of the science of systematic botany.

Amateur Botany.—With the growth of the different sciences there is a desire on the part of many people to study them from the amateur's standpoint. Probably no other science, except possibly geology, has so captured the interest of the amateur as botany. Such studies could be made in any field of this science, but systematic botany is the one with the greatest appeal. This is largely due to the fact that it gives an opportunity for satisfying the human desire to collect. While some amateur collections of plants serve only a temporary purpose, others are of great value and contain thousands of specimens accompanied by important ecological data. Usually such collections are finally donated to educational institutions where they will be protected from fire and other destructive agencies.

More and more the spirit of service is pervading the scientific world. With increasing effectiveness representative men in each science will apply their work and that of their colleagues to everyday life. In harmony with this tendency, the systematic botanist of tomorrow will add to the names and classification of plants much information of value to the human race.

CHAPTER I

EVOLUTION IN RELATION TO TAXONOMY

Several bases of classification have come into use, each designed to serve a special purpose. Some of these grew out of the economic uses of plants; others were founded on gross structural resemblances such as habit of growth—trees, shrubs, vines, and herbs. All these systems were fragmentary and incomplete, and those plants that did not fit the classification or had a different interest were ignored. For example, plants not regarded as medicinal received little consideration by the early herbalists. At the present time many wild plants that are not known to be either beneficial or harmful to agriculture are ignored even by those whose scientific training in agriculture has included considerable botany. Only one system of classification has made any pretense to completeness, and that is the one now in use which is based on natural relationships.

Before the conception that existing species originated by evolution had been proposed, "natural relationships" among plants and among animals were described. Certain families such as the Umbelliferae, Compositae, Gramineae, and Leguminosae were recognized through morphological similarities in flowers, inflorescences, leaves, etc., but the expression "natural relationship" did not have the significance that it now has. It meant merely similarity of parts. That the early conceptions of relationship among living things were based largely on comparative morphology is fortunate, for this has been found to be one of the best criteria of phylogenetic relationship.

IDEALS IN CLASSIFICATION

There are three conceptions of classification that must be understood in studying systematic botany.

1. Natural classification refers to the relationships that exist among plants as a result of evolutionary development, regardless of man's knowledge of the subject. These natural relationships

actually exist and would exist if there were no human beings on earth to study them.

2. Taxonomic classification is the result of man's efforts to express or describe natural classification and put it into form for discussion and use. Inevitably it is imperfect, incomplete, and subject to improvement, for it is built on incomplete evidence and even personal opinion concerning natural classification.

3. Artificial classification is a grouping, generally for convenience, that does not pretend to express natural relationships. Often it is the result of using a single character as a basis for classification rather than a combination of characters, which is now recognized as the surer method of bringing out actual relationships. Making a single class that would include all thallophytes, or all spermatophytes that lack chlorophyll, but no others would result in an artificial group.

Methods of Classification.—The *ideal* classification must embody two qualities. It must show actual phylogenetic relationships, and it must be reasonably convenient for practical use. If it fails to show true relationship, it is artificial and does not satisfy the discriminating thinker, although it may be convenient for use. Too often, however, as in the bacteria and some groups of fungi and algae, an artificial grouping has had to suffice until a taxonomic classification could be perfected. If, on the other hand, a natural system is too involved and too difficult of comprehension, and especially if, in addition to these faults, the phylogenetic evidences are incomplete and debatable, such a system fails to gain general acceptance and may have to give way, at least temporarily, to one that is more artificial. Many botanists believe that different classes of fungi originated from as many groups of algae not closely related to each other and that a natural phylogenetic classification should show a closer relationship between certain fungi and certain algae than between the different groups of fungi. Nevertheless, they continue in actual practice to treat the fungi as if they were a homogeneous unit.

One of the advantages of a phylogenetic classification over an artificial one is that it is safer to generalize in related groups than in unrelated ones. For example, if one is well informed concerning a few species of Pinaceae, Gramineae, Leguminosae, or Cucurbitaceae, he can assume the likelihood that some of his knowledge will apply to other members of the same family,

although some verification will be necessary and differences in detail must be expected. On the other hand, if all plants with compound leaves were considered to be a family, this would give us an artificial group and no generalization would be safe except one regarding the leaves. Fortunately, in most of the spermatophytes phylogeny and convenience can be fairly well combined.

Evolution as a Basis for Classification.—The relationships of species or other groups are determined by the genetic lines running back from them to a common ancestor. Other things being equal, the shorter the genetic lines (in time) and the nearer the two species being considered are to the point where the two merge into a common ancestral line, the closer the relationship. However, if the two species are much alike, indicating that the two genetic lines have run nearly parallel, we call this condition parallel development, or parallel evolution, and these species are commonly thought of as being more closely related than others that show greater differences and consequent divergence of phylogenetic lines that may have been much shorter.

In considering evolution as a basis for classification, a student in any branch of biology has to make a decision among three alternatives: (1) to reject the hypothesis of evolution and with it the idea of true natural relationships, (2) to accept this hypothesis blindly on faith in the judgment of his instructor, or (3) to look into the evidence bearing on the subject. The last named is the scientific method.

EVIDENCES OF EVOLUTION

At the outset the meaning of organic evolution should be made clear. Evolution is believed to have produced all existing forms of plant and animal life from more ancient forms that were fewer in number and simpler in structure than those of the present day. It is not held that one group as it exists today came from another group as it exists today, but that similar groups had a common ancestor more or less like both.

A great deal has been written in recent years on the evidences of evolution and also on the methods of its operation, concerning which some half-dozen plausible theories have been proposed. Space limits us here, however, to a brief outline of the best accepted evidence on which the belief in evolution is based.

Geological Evidence.—It is well known that the surface of the earth is not smooth and unchanging. In the past slow but profound changes have taken place. Land has been lifted out of the sea, and mountains have been lowered by erosion—the materials thus removed being finally deposited in the ocean as layers. These layers have later been lifted to form new mountains, and the process has been and is being repeated again and again. Some of the strata of earth and rock that have thus been formed contain many fossils, the remains or prints of prehistoric plants and animals. The forms of life represented by these fossils give an important historical record of the kinds of living things that have existed on the earth during the past ages. If all kinds of plants and animals, higher and lower, had been created and established at the same time and place, we should expect the fossil-bearing layers, both older and newer, to contain representatives of all of these, but such is not the case. The older strata, those formed before the Cambrian era (see frontispiece and table on pages 12-13), contain limestone, graphite, and fossils of primitive forms of life only, especially marine algae and invertebrate animals. Strata not quite so old, those of the Paleozoic era, bear fossils of complex invertebrates, lower vertebrates, seaweeds, pteridophytes, and gymnosperms. Not before the Mesozoic era were fossils of mammals and angiosperms produced, while the apes and man left no fossils below the younger layers of the Cenozoic era.

It is generally accepted as a fact that the time from the Archeozoic era to the Cenozoic era covered hundreds of millions of years and that new species of plant and animal life kept appearing on the earth throughout that extensive span. This leaves us with two alternatives: (1) that direct creation was repeated many times throughout all that vast period of time, up to the present, thus producing the hundreds of thousands of species now in existence and others that have become extinct, or (2) that the species that first came into existence were relatively few and simple and that they gave rise to newer and more complex ones by evolutionary processes. The latter seems the more plausible and is widely accepted.

Morphological and Anatomical Evidence.—The members of different groups of animals and plants show striking similarities in fundamental structure but vary in lesser details. The spinal

UPPER HALF OF PALEONTOLOGICAL RECORD[1]

Psychozoic era: Dominance of man and herbaceous plants	Recent or postglacial time 20,000 yr.		Receding of polar ice caps, moderate rise of temperature, temperature zonation, aridity of intermontane regions. Wane of forest trees, dominance of herbaceous plants and of civilized man
Cenozoic era: Dominance of mammals and angiosperms	Late Cenozoic (Neogenic) period 25,000,000 yr.	Pleistocene or glacial epoch	Ice caps and glacial conditions extending from poles into temperate zones. Extinction of many large mammals and trees. Survival of hardy adaptable types, especially herbaceous plants. Elevation and extension of continents. Beginnings of civilization
		Pliocene epoch	Moderate cooling of climate with increasing aridity. More restriction of forests. Appearance of man. Elevation of the Andes
		Miocene epoch	Slight cooling of climate with aridity in places. Decrease of forest areas. Increase of grasses and culmination of mammals. Elevation of the Swiss Alps
	Early Cenozoic (Paleogenic) period 60,000,000 yr.	Oligocene epoch	Warm, moist climate. Zenith of forest areas. Increase of higher mammals and of birds. Elevation of the Pyrenees
		Eocene epoch	Climate cool and semiarid, then warm and humid. Extension of forests into polar regions. Wane of archaic mammals. Appearance of marine mammals and of primates. Continued elevation of the Rockies
Mesozoic era: Dominance of reptiles and gymnosperms	Upper Cretaceous period 100,000,000 yr.		Fluctuating climate. Increase in modern forests, including birch, walnut, and maple. Extinction of dinosaurs. Increase of mammals. Extensive coal deposits from gymnosperms and some pteridophytes. Elevation of the Rockies
	Lower Cretaceous period 120,000,000 yr.		Tropical climate, depression of land with invasion of seas continuing into Upper Cretaceous. Earliest known palms and grasses. Beginnings of modern forests including poplars and sassafras. Zenith of dinosaurs
	Jurassic period 145,000,000 yr.		Gradually rising temperature; colder at poles. Widespread warm seas. Increase of dicotyledons. Appearance of numerous toothed birds and flying reptiles. Dinosaurs predominant. Beginning of the Sierra Nevadas
	Triassic period 170,000,000 yr.		Warm, semiarid climate. Shallow, warm seas and lagoons. Gymnosperms and pteridophytes continuing to wane but still dominant. Probable origin of dicotyledons. Rise of dinosaurs. Appearance of mammals. Extended lands
Paleozoic era: Dominance of fishes and pteridophytes	Permian period 210,000,000 yr.		Dry, glacial climate especially in Southern Hemisphere. Appearance of the Glossopteris-Gangamopteris flora. Gymnosperms beginning to wane but still dominant. Great mortality of specialized animals and plants. Land vertebrates increasing. Extensive salt deposits
	Pennsylvanian (Upper Carboniferous) period 255,000,000 yr.		Climate warm and humid. Pteridophytes reach zenith and begin to wane; gymnosperms reaching zenith. Increase of reptiles and insects. Amphibians abundant. Extensive coal deposits from pteridophytes and gymnosperms
	Mississippian (Lower Carboniferous) period 285,000,000 yr.		Land climate temperate, seas cool. Winter climate in mountains. Gymnosperms approaching zenith. Sharks and crinoids abundant. Amphibians increasing. Thin coal deposits
	Devonian period 325,000,000 yr.		Warm climate with moderately dry air. Rapid increase of pteridophytes and gymnosperms. Appearance of amphibians. Fishes predominant. Earliest fossil record of land plants
	Silurian period 350,000,000 yr.		Warm climate, semiarid in certain regions. Probable increase of pteridophytes and gymnosperms. Appearance of scorpions, myriapods, and lungfishes (first air-breathing animals)
	Ordovician period 410,000,000 yr.		Continued warm climate. Possible origin of gymnosperms and increase of pteridophytes, but marine algae still dominating. Corals, bryozoans, cephalopods, and brachiopods abundant. Appearance of armored fishes
	Cambrian period 500,000,000 yr.		Warm, uniform climate over the earth. Possible origin of pteridophytes. Marine algae dominating. First known marine animals (trilobites and brachiopods)

[1] The data recorded in this table are derived from the character of the earth's strata and the fossils that they contain. In some cases the oldest known fossils are of such specialized forms as to leave no doubt that they had a long line of ancestry in the same phylum; hence the probable origin of that group is indicated at an earlier period. The figures given are estimates of the time from the dawn of each period to the present. Since the fossil records are fragmentary, the table must be looked upon as expressing prevailing opinion, and subject to some revision.

column in all vertebrates and the same number of limbs in mammals, birds, and reptiles suggest relationship through a common ancestor. In all the vertebrates, except the most primitive, there are four limbs, sometimes in a rudimentary, sometimes in a highly specialized, condition, and the skeleton of the arm and forefoot, for example, compares almost bone for bone with that in such superficially different structures as the walking organs of the bear, the swimming flippers of the whale, the wings of the bat, and the grasping organs of man.

In the spermatophytes every part of the sporophyte is some form of root, stem, or leaf; and every plant has all three of these structures, though they may differ greatly in form and function. The chromosome number in these parts is always diploid. Given the general characteristics of the fibrovascular system, one can infer correctly in almost every case the number of cotyledons and the venation of the leaves. The tissues of normal leaves show a general similarity of plan with palisade cells above, in which respect they differ from cladophylls, which are leaf-like stems. The position of buds in the axils of leaves at nodes is likewise uniform.

This similarity of ground plan points to a development from ancestral forms by a process of evolution, which would be likely to modify existing structures rather than to create new ones.

Embryological Evidence.—A special kind of anatomical evidence is found in the embryological development of higher animals. The ancients believed that, in general, living things started with an appearance and structure much like miniature adults, growth and development being merely processes of enlargement of each individual organ. Scientific observation has revealed that such is not usually the case. The fern, beginning with the germinating spore, first resembles a green alga. From this develops a small thallus like those of the liverworts. This prothallium, in turn, is replaced by the leafy, mature form with which all are familiar.

The frog in its metamorphosis goes from a one-celled state through the tadpole stage, more like fish than amphibian, and changes to adult form by loss of tail and gills and development of legs and lungs.

Insect larvae have no wings, not even rudimentary ones, and resemble worms, which they are often called. But these larvae,

by losing certain leg-like structures, taking on permanent legs and wings, and developing a definite segmentation, become in adult life strikingly different creatures.

Ontogeny is a term used to express a series of embryonic stages of individuals such as those just described. *Phylogeny*, on the other hand, expresses the evolutionary history of a race of beings from remote ancestors. Haeckel's "law of recapitulation," translated into English, states that "Ontogeny is a brief repetition of phylogeny." This law has been highly useful in tracing relationships in animals and plants. The early stages of the advanced form and that of the simple form, presumably ancestral, are much alike, but the higher form continues its development farther and thus produces a complex individual.

Vestigial Structures.—In a close examination of the higher plants and animals one finds many structures wholly useless and sometimes actually detrimental to the individual. Of what use to plants are scale-like leaves on rhizomes and tubers, stamens without anthers, and the antheridial cells of germinating pollen grains? Why should the legs of the horse include so many little bones, some of which by pressure against others become inflamed and cause splints and spavins? Why the easily infected vermiform appendix, the coccyx bones, and the scattered body hairs of the human being? Why so many useless structures in higher forms of life and so few in lower forms? As a result of direct creation such structures would seem absurd.

Evolutionary development, however, would almost inevitably be accompanied by such vestiges of once useful organs. Great and varied environmental changes have taken place during the eras since life appeared on the earth. The changed conditions profoundly affected the existing plants and animals. Some species unable to adjust themselves were exterminated, and but for their fossil remains we should never know that they had existed. Other species became adapted to the new conditions by structural modification. Some organs, such as bones, for example, were lengthened, shortened, or otherwise modified, and in some cases were entirely lost. Useless structures became encumbrances, and the species best fitted to survive were those in which these superfluous parts were rapidly reduced and made unobtrusive or entirely lost. It sometimes happened, however, that another change of environment reestablished a need for the

organ in its original or equivalent form. If it was too far gone or too greatly modified, the victim perished, as doubtless happened in numerous instances, for by the law of irreversible evolution (see page 28) animals and plants do not ordinarily go back to earlier states. Had the bodies of living things been so unstable that organs would quickly and entirely disappear with a brief change in the climate or the food supply, organic adaptation would have been oversensitive and caused destruction rather than protection. That myriad forms of life did survive profound environmental

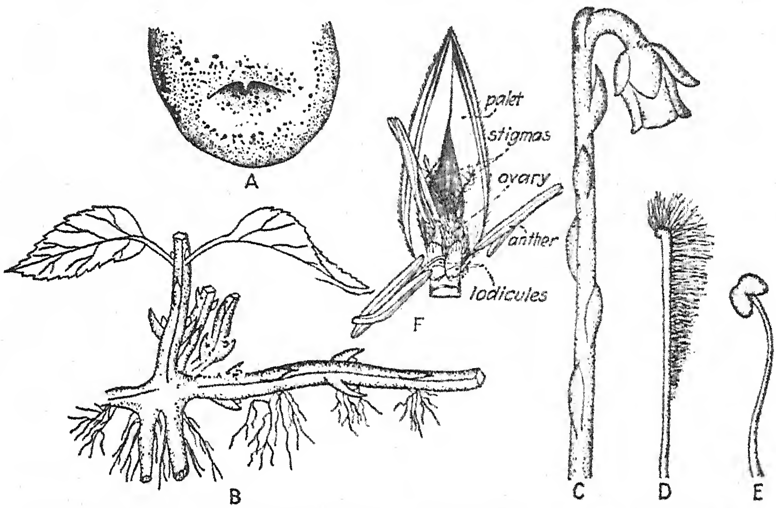


FIG. 3.—Vestigial structures in plants. *A*, potato tuber with a scale-like leaf at an "eye." *B*, rhizome of peppermint with scale-like leaves. *C*, Indianpipe, which is colorless and saprophytic and has scale-like leaves. *D*, staminode—vestige of stamen in beard-tongue, in contrast with normal stamen. *E* and *F*, lodicule—vestige of petal of wheat. (*F*, *after Robbins.*)

changes is evidence of the tenacity with which unused organs persisted. Modification rather than destruction of organs appears to have been the fortunate rule. Furthermore, by this hypothesis vestigial structures would be more frequent in the versatile, highly complex spermatophytes and vertebrates and more rare in the simple, conservative, lower forms.

Thus it can be seen that by a theory of evolution these vestigial or rudimentary structures can be explained naturally, while by a theory of direct creation they are inexplicable and inharmonious.

Recent Productions.—It must not be supposed that evolution has come to a standstill, that it began when the world was young,

continued for a few million years, and then ceased to operate, leaving us with a great array of unchanging species. There can be no doubt that it has been continuous from the start, is still going on, and will continue into the indefinite future. That new species of animals and plants are forming all the time is a well-accepted fact supported by observation and experiment. Variation from the parental characters appearing in offspring, followed by the survival of the fittest (a Darwinian principle), still goes on in nature and can be hastened experimentally by the geneticist.

Of the offspring obtained by crossing related subspecies and species, many fail to reproduce or are poorly constituted to meet the conditions of their environment and soon disappear; some are sterile, and others, especially among plants, are fertile, surviving and multiplying; and their new combinations of inherited characteristics, if firmly established, may be sufficient to constitute them new species. The mutation theory of de Vries assumes that most evolutionary changes take place in this way.

These processes go on among wild plants, and some of the resulting products are collected and given specific or varietal names. By the same processes other products are made by plant breeders. Varieties of corn, fruits, and vegetables, wonderful flowers, breeds of dogs, pigeons, and goldfish—all these and many more existing forms of life we know have actually come from ancestry that was very different. That we now call these different cultivated and domestic forms varieties rather than species is of little significance, for there is no doubt that many of them, if found wild, would unhesitatingly be given different specific names.

The fact must not be overlooked that these recent productions have been made in a relatively brief time. Compared with the duration of life on the earth, the existence of civilized man has been as a day is to a century. One could not expect, therefore, that a considerable number of new species would become established in so brief a span.

ACCEPTANCE OF THE DOCTRINE OF EVOLUTION

The popular conception that Charles Darwin was the first to suggest the origin of species through a modification of previously existing species is an error. During the first half of the

nineteenth century at least a score of writers,[1] including both scientific men and theologians, gave some expression to this idea, mostly in the form of brief comments incidental to a discussion of some other subject. The tendency of these early writers was to express their belief, sometimes supported by evidence, that certain species had originated by successive changes in ancestral lines without claiming that such a method of origin was universal or even general. A few even went so far as to include man among the products of evolution, and it seems surprising that they remained unchallenged.

FIG. 4.—The Darwin-Wallace medal given by the Linnaean Society in recognition of the work of these two great pioneers in the study of organic evolution. (*Courtesy of Popular Science Monthly.*)

In 1858, Alfred Russel Wallace, a young English naturalist, sent to his older and better known countryman, Charles Darwin, a hastily prepared manuscript setting forth his views on the origin of species through variation and natural selection, closely similar to the unpublished conclusions of Darwin but reached independently. Upon the insistence of his friends Darwin prepared a summary of his own work, which was published[2] jointly with the paper submitted by Wallace. This was followed a year later by Darwin's book in two volumes on the "Origin of Species," which was the product of some 20 years of study. It is a matter of history that the theory of evolution, when first set forth by

[1] Most of these are mentioned in the Historical Sketch of Darwin's "Origin of Species."

[2] DARWIN, C., and A. WALLACE, On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection, *Jour. Linn. Soc. London*, **3**: 53, 1858.

Darwin and his associates, was seriously challenged because it seemed so revolutionary. At the present time, however, it is given the same recognition as that accorded to other principles in all fields of science. Its adoption has revolutionized the classification of plants and animals, and what is most needed now is more information as to the methods of its operation and the course it has followed, in order that we may complete our knowledge of phylogenetic taxonomy.

THE MECHANISM OF EVOLUTION

The fact that organic evolution takes place is generally accepted, but the explanation as to what causes it to go on has been difficult to ascertain. The endeavor to do so has involved numerous researches in genetics, cytology, and ecology, and yet our knowledge on the subject is far from complete. While it is generally believed that the rate at which evolution operates has varied appreciably during different periods of geologic time, it is also thought that in terms of a human lifetime it has been very slow.

In the evolutionary process many patterns and materials have been used, most of which have been discarded. The present life on the earth is the product of this long process of trying, sorting, selecting, and discarding. The experimental biologist interested in this subject is able to study only the relatively elemental steps in the process, such as those that take place within the species. On rarest occasions he has been able to reproduce artificially an existent natural species, but the genetic relationships of genera, families, and higher groups at present are closed to experimental investigation. Their evolution has gone so far that it is doubtless now impossible to repeat the steps with the living forms that remain on the earth.

Variation and Natural Selection.—Darwin recognized two great principles of evolution, variation of the offspring from the parental characters and survival of the fittest by natural selection, but he did not fully understand the explanation of either. Variation is the active agency that develops new forms upon which evolution may build; natural selection is ever operative upon this variation, eliminating many forms and perpetuating, in general, those best fitted to survive in that environment in which they find themselves.

The Kinds of Natural Variation.—Variation in plants is of two sorts, heritable and nonheritable. Failure to differentiate clearly between these has been a source of some confusion in taxonomy. The heritable variations, which are transmitted from parent to offspring, are the only kind that have significance in evolution. The nonheritable variations are acquired during the life of the individual as direct effects of the environment. These are temporary and reversible and consequently of no significance to either evolution or taxonomy, but it is not always possible to distinguish them from heritable variations without performing an experiment. Undoubtedly, new specific names have been given to some of these, and they can be found in herbaria so named.

Variation is common to all plants whether they reproduce asexually or sexually. It is to be expected, of course, that there is relatively much less variation among those forms that depend upon vegetative reproduction, whether it be by simple fission, as in the lowest plants, or by aerial bulblets, layering, or development of seed without fertilization (apomixis), as in the higher plants. Self-pollinated forms are likewise less variable than those that must be cross-pollinated.

The genetic variations among plants of a given kind in a single population are often trivial in appearance and in themselves of no evolutionary or taxonomic significance. When plants of all the populations of a common hereditary pattern in an area are considered together, however, and compared with those of a somewhat different pattern found growing in another climatic region, then the evolutionally significant climatic races or subspecies of a single species are disclosed. The hereditary patterns of different species are ordinarily less similar than those of the climatic races of one species, but the degree of morphological difference alone is not the final mark of a species. The genetic relationship is a sounder criterion of origin than is morphology but more difficult to determine.

The species of a genus have a number of characteristics in common that mark them as a group distinct from other groups. The explanation for this lies in their common evolutionary origin. Experiments show that in most genera many species are still closely enough related to be able to hybridize to some extent. In this way they intermix their hereditary materials slightly and retain many characters in common. When one group is no longer

able to hybridize with others in the same genus, it has attained the genetic mechanism for becoming an independent genus. In most cases, however, perhaps many thousands of years are required for it to differ sufficiently to be considered a distinct genus.

It has been noted that some species, *e.g.*, the maidenhair tree, *Ginkgo biloba*, a gymnosperm, and sassafras, *Sassafras variifolium*, a small deciduous tree common in the eastern United States, have not undergone any important variation for millions of years, while in some genera, *e.g.*, *Oenothera*, *Senecio*, *Datura*, *Rubus*, *Crepis*, *Viola*, and *Carex*, and in some cultivated plants, including barley and maize, variations are very common. Obviously, such groups lend themselves readily to the work of the plant breeder and the geneticist in their endeavor to produce new varieties. An illustration is found in the genus *Rubus*, which includes blackberries, raspberries, etc., from which the newer loganberries, youngberries, and boysenberries have been produced.

Since all stages in the evolutionary process are found in nature, it is not surprising that there is some disagreement as to what rank to accord different groups. Because the morphological gaps become greater as the rank of the group is increased, most confusion surrounds the subdivisions of species, and the delimitation of species themselves. Much less is connected with the separation of genera, and there is considerable uniformity of opinion as to the delimitation of families.

The Mechanism of Variation.—A study of the many kinds of heritable variations and their transmission from generation to generation rightly falls within the field of genetics. However, the taxonomist who is trying to classify the end products of evolution from the viewpoint of phylogeny also has an interest in the mechanism of evolution.

As each individual is usually the product of the union of two sex cells, one contributed by the male and the other by the female parent, all heritable variations must have come through these. Variation arises in several ways. In the first place, it is obvious that the offspring of two unlike individuals cannot be identical with both of them. Its appearance will largely depend upon the interaction of the hereditary substances received from each parent. Consequently, the offspring may look a little different from either parent. In general, the more unlike the parents

are, the greater the variations within the offspring are apt to be.

Secondly, the hereditary substance itself is subject to occasional change. While this is usually first noted in the products of reproduction, it may have been initiated in the "resting" nuclei prior to reproduction. This is apt to give rise to new characters not found in either parent. Such spontaneous origin of new variation is known as mutation. At one time mitosis and meiosis were supposed always to follow a definite pattern, but we know now that such is not always the case, that even the chromosome numbers may change. Such abnormalities may result in partial or complete sterility in the offspring, or in morphological changes. Both hybridization and mutation are important building stones in the evolutionary process.

Different kinds of mutation occur, all of which cause variation. Most of them take place in the structures within the nucleus that carry the hereditary substances, *viz.*, the chromosomes. The number of chromosomes may change, or their parts may become rearranged, or their contents may mutate. Changes in number are detectable under the microscope and rearrangements often are; but the changes in content, which are usually slight, else death results, are invisible except as the effects can be observed in the offspring.

When cross-pollination takes place, whether it goes on in nature or is carried on by man, various results may follow, depending on the character of the parents. Because of genetic barriers, *i.e.*, incompatibility of the gametes, shortness of the pollen tube, etc., fertilization may not take place and no seeds will be formed. If offspring is produced, it may be sterile, or partially so, or lacking in vigor and unable to cope with its environment. With proper chromatin combinations there may be no genetic barriers and vigorous offspring may be produced, which, if isolated in a suitable environment, may form new lines that will in time develop into new subspecies or even new species.

Some causes of mutation are known, but many others remain undiscovered as yet. Some mutations are caused by environmental factors such as temperature changes, aging the seed, and certain radiations such as X rays, all of which may affect the chromosomes and induce variation in the offspring. Other mutations are induced by genetic causes such as the hybridization of widely unlike forms.

The fundamental unit in heredity is the gene, the element of hereditary material upon which some morphological or physiological condition of the organism depends. Very many genes are aligned along each chromosome. A mutation in one gene is seldom very significant to the organism, but many such mutations accumulated over a period of time may significantly alter the composition of a given form.

After years of research there is still a difference of opinion among geneticists as to whether new species originate more commonly from pre-existing ones by sudden major mutations or by the gradual accumulation of many minor heritable differences, such as gene mutations.

The Importance of Isolation.—The innumerable variations that arise through mutation and are recombined in various patterns through hybridization are continually subjected to the forces of natural selection. New forms are unable to exist for long in competition with the old unless their identities are maintained by genetic or environmental isolation of some sort. Genetic isolation is brought about by internal barriers to the successful continued crossing with the pre-existing forms. Such barriers include incompatibility of the sex cells, different dates of flowering, etc. Environmental isolation is largely spatial or geographic.

Evolutionary Processes.—As a rule, the more closely related that plants are to each other, the more likely they are to be capable of successful crossing. Plants from different families cannot ever be crossed, and those of different genera only rarely. It is often possible to cross species of the same genus, but this may be prevented by genetic barriers such as differences in the number or composition of the chromosomes or in the character or positions of the genes. Subdivisions of the species, *i.e.*, related subspecies, varieties, races, etc., ordinarily cross without difficulty.

Hybrids between two plants of the same species may show considerable morphological variation, but they are ordinarily fully fertile. In this respect they differ markedly from hybrids between different species, which are at least partially sterile, producing inferior offspring. The hybrids between genera, in the few instances in which they are obtained, prove entirely sterile.

The multitude of variations produced in nature are subjected to selection by the environment, and the unfit are eliminated, often very promptly. New forms become well established only

. . . they are in harmony with their environment.

As climates change through periods of time, new environmental niches may become available for occupation by suitable forms, and the old habitats become much modified. If the species is to persist, one of two things must happen: either it migrates into habitats still favorable to it, or its capacity for variation is sufficient to permit it to develop new forms in harmony with the changing environment. Extinction has been the lot of innumerable forms that have faced environmental change with too little genetic capacity for variation.

Even though there are now hundreds of thousands of species of plants and of animals, there are not nearly so many as might be expected if one considers the frequency with which mutation and hybridization take place and the millions of years that evolution has been going on. Researches in paleontology have shown that many species of plants and animals that were once well established on the earth later became extinct because of environmental changes, increase of enemies, etc., and undoubtedly there have been innumerable hybrids, mutants, and variants that did not persist long enough to produce fossils and so were lost entirely.

ACCOMPLISHMENTS OF EVOLUTION

The millions of individual plants and animals covering the earth and constituting thousands of species are looked upon as so many products of evolutionary development. What the first form of life was, whether it originated at a single point or several, and whether or not plants and animals had a common ancestry are questions that cannot be answered now. Every species of plant and animal now on the earth shows a complexity of structure far beyond what must have been possessed by its remotest ancestor. It is doubtful if that ancestor was even a well-organized cell.

Much evidence points to the conclusion that during the vast eras of organic development periods of accelerated progress took place. Conspicuous in the plant kingdom was first the production of chlorophyll, and millions of years later the structural adaptation to a terrestrial enviroment and the advent of an alternation of generations of the progressive character found in bryophytes and pteridophytes. Prior to these last two epoch-making events changes among the marine plants appear to have

been relatively slow. With a land-and-air environment and a progressive sporophyte alternating with a waning gametophyte in each life cycle, increase in complexity appears to have taken place by leaps and bounds.

It is a significant fact that while some forms progressed rapidly others were relatively stable. Had all changed equally, we should have no lower plants and animals now. Doubtless all have changed more or less from their ancestral forms but some relatively little. This fact is a great help in the study of phylogeny, for the progressively higher forms may be compared to a series of pictures of evolution, taken as it marched past.

PROGRESSIVE AND REGRESSIVE DEVELOPMENT

As a matter of convenience and in accord with our narrow human standards we say that phylogenetic lines have either progressed or degenerated. These terms must be used with caution and may be misleading if the situations to which they apply are not closely analyzed.

Indications of Upward Development.—Upward or progressive development generally implies an increase in qualities beneficial to the race.

Increase in size is usually looked upon as progressive. In general, the higher plants and animals are larger than the lower ones, though there are numerous exceptions. Tall plants may be able to reach the light where shorter ones would be deprived of it. Large animals may be able to overcome smaller ones in combat, other conditions being equal. Size, however, may become a hindrance, especially among animals, where food is scarce or where the ground has become too soft for locomotion. In all likelihood this aided in the extinction of certain huge prehistoric reptiles and mammals. The fact that trees are waning while herbaceous plants are increasing suggests a condition analogous to that found in the animal kingdom. It may be that as conditions are now on the earth herbaceous plants are better suited to survive than woody plants.

Increase in specialization is a more certain indication of advancement. The developments of heterospory, of stomata, of root hairs, and of palisade tissue in leaves, to take the place of less differentiated structures, are familiar examples. In the lower

plants one cell or a simple filament may perform the functions of all of these but do it less efficiently. Organs specialized for "division of labor" are characteristic of both higher animals and higher plants.

Quite clearly there may also be danger in specialization, either because the specialized organ becomes an encumbrance, or because of the fact that with specialization of a given structure to do certain work there comes to be a lessened ability on the part of other structures to do equivalent work. When conditions are right for the specialized organs to function effectively, the plant prospers, but with altered conditions more conservative structures may save the race. Two examples will make this clear. (1) If conditions were favorable for insectivorous plants to obtain most of their nourishment from their prey and other food were scarce, specialization of "fly traps" with the inevitable reduction of other organs of nutrition would be advantageous; but should the supply of insects fail, the more conservative ancestral forms that could obtain their food materials directly from soil and air would be more likely to survive. (2) Xerophytic structures are well adapted to arid conditions, but a xerophyte in a swamp would be worse off than a mesophyte.

It is now agreed that the plants and animals with organs highly specialized in one direction are not usually the ones from which higher groups evolved. These greatly specialized groups more often form side branches to the main genetic stem. It is doubtful whether *Pilobolus*, *Hydrodictyon*, *Marchantia*, or the specialized insectivorous plants have given rise to any important group or, indeed, if they ever will.

Specialization of animals has far exceeded that of plants, particularly in the various methods of locomotion and in the marvelous development of the nervous system and special senses. Correspondingly, they appear to have suffered even more than plants from excessive specialization in directions that were an obstacle under changed environmental conditions.

Forms of Degeneracy.—It is in a study of so-called degeneracy that we need to think our way most carefully. It is usual to regard any loss of structures or of functions once useful, or any increased tendency to be dependent on other forms of life, as degeneracy. The question is largely one of definition and interpretation. The conspicuous example of degeneracy in the plant

kingdom is loss of chlorophyll. It is probable that the first living things on the earth had no chlorophyll and that its acquisition was one of the greatest events in the history of the organic world. The ancestors of the fungi appear to have acquired it, but in their change to fungi they lost it. So also with the Indianpipe and a few other angiosperms. If planted in an environment of abundant and suitable organic matter, with little light, these plants thrive better than their chlorophyll-bearing relatives; but if stranded in an inorganic environment they perish. It is a well-established fact that plants that have completely lost their chlorophyll and the plastids containing it never regain them. Such plants represent independent species that have degenerated into saprophytes.

Parasitism is another form of degeneracy common among plants and animals. *Strict* or *obligate* parasites thrive when associated with certain hosts *but not elsewhere*. Such obligate parasites are, however, rare. Most parasites, especially fungi, retain saprophytic power, which they use in times of necessity, and many of them live a saprophytic life more commonly than a parasitic life. Saprophytic fungi often thrive better than algae growing in the same region, and in acquiring a saprophytic habit they have gained more than they have lost.

It is not safe to class all loss of parts as degeneracy, for sometimes this loss is a form of specialization. Several examples may be cited. (1) In pteridophytes a megaspore mother cell produces four functional megaspores, but in most spermatophytes it forms four cells that are *potential* megaspores, one of which develops at the expense of the others, which fail to enlarge and disappear. (2) Bisexuality in angiosperms is looked upon as a primitive condition, while unisexuality, by the evolutionary loss of stamens or carpels from the flowers, is more advanced. (3) Loss of petals (apetaly), in some cases at least, is considered an indication of advancement. Probably the term "regressive development" is more fitting than "degeneracy."

When it is remembered that all vestigial structures (see page 15) are products of degeneracy, that they are usually the result of adaptation to a changed environment, and that they are especially prevalent in the higher forms of life, we see that it is necessary to give a liberal interpretation to what is commonly called degeneracy.

Evolution Is Irreversible.—In 1892, Louis Dolle, a Belgian paleontologist, put into concrete form a principle that had been vaguely felt by others. As restated in 1901, it is as follows: "An organism never exactly renews a previous condition, even if it finds itself placed in an environment identical with one through which it has passed. But, by virtue of the indestructibility of the past, it always retains some trace of the intermediate stages which it has traversed." This "law of irreversible evolution" has many applications in both botany and zoology. When organisms have become profoundly changed through adaptation to environment and then have been resubmitted to the earlier conditions, they have not gone back to ancestral types but have become adapted through new modifications. We hold that at one time all plants were aquatic, that some of their progeny developed terrestrial habits and structures, and that some of the progeny of these terrestrial plants became aquatic again; but in doing so they certainly did not become marine algae like their ancestors.

A few examples of apparent reversibility, however, may be found in certain organs among flowering plants. There is little doubt that primitive evergreens gave rise to deciduous plants, some of which in turn became evergreen, as illustrated by the holly, Oregongrape, and live oak. Apparently quite frequently, plants with one leaf at a node gave rise to others with two leaves at a node, although in all probability all came from ancestors that were uniform with respect to the arrangement of leaves on the stem. Broad leaves have given way to narrow ones and vice versa. Furthermore, herbaceous plants have arisen from woody forms, and in a few cases they have given rise to woody forms again. It is true that the newer product is not an exact reproduction of the ancestral one with respect to the quality in question, but, nevertheless, the apparent reversal may mislead the student of evolutionary tendencies.

It is quite possible that minor changes, especially those of physiology, require some time to become permanently established, and that before that time is complete, the plants, in adaptation to a change in the environmental conditions, may revert to an original condition. In the main the law holds true, however, and is a great guiding principle. It may seem to conflict with the belief in "reversion to type," but so little is known of the underlying principles of this so-called reversion (except as

an expression of recessive Mendelian characters or recurrence of primitive factorial combinations) that it does not weigh heavily against Dolle's law.

In the further development of the topic of taxonomy in later chapters, phylogenetic arrangements will be followed as much as possible, but since the scope of the book is restricted chiefly to the Spermatophyta, many perplexing problems of relationships among the lower plants will receive only incidental consideration.

CHAPTER II

METHODS USED IN THE IDENTIFICATION OF FLOWERING PLANTS

When one collects flowering plants and wishes to determine their species among the thousands to which names have been given, the magnitude of the problem might seem to make it hopeless. The methods, however, have been worked out so well that the average college student, with a background of one course in general botany, can learn to perform the task rather easily, except for a few kinds that belong to the more difficult large genera, such as *Astragalus*, *Poa*, *Carex*, *Pentstemon*, and *Senecio*, and many species in these genera are not difficult to identify.

No Short-cut Method.—The greatest difficulty is had by the amateur who does not know the morphological terms by which plants are described. There is great demand for a small, handy book with colored illustrations and nontechnical descriptions from which any flowering plant can be easily and quickly identified by those who have made no study of botany. Unfortunately, such a book could not possibly be made; for the number of species is so great that it would have to be very large, its cost would be prohibitive, and the amount of time required to sort through all of the descriptions and illustrations for the plant in question would be discouraging. Furthermore, some species are so much alike in *general* appearance that even colored photographs would fail to bring out distinctions that are based on small or concealed parts; and if the descriptions were written in common terms, these distinctions could not be made.

The best attempts in this line are books and pamphlets that picture and describe some of the more conspicuous and interesting plants of a limited region and omit the others. They are useful but far from satisfactory.

Names.—Popular books on plants often give both the common and the scientific names, but while those species that have been studied have all been given scientific names, thousands have never

been given common names that distinguish them from others in the same genus. The genera *Astragalus*, *Carex*, *Lupinus*, *Rosa*, *Senecio*, and *Poa*, for example, all contain many species which do not have common names that distinguish them one from another.

The Securing of Suitable Specimens.—The difference between the ease of identification of poor specimens and of good ones is very great, and it is well worth while to collect and preserve carefully. As a rule, fresh specimens are more easily studied than dried or wilted ones. If the student is required to hand in a small herbarium as a part of his assignment, he should by all means press some of his specimens as quickly as possible in a field press, if one is available, and keep others fresh in a covered pail or a vasculum for detailed study and identification. Small portions of plants, bearing flowers and a few of the upper leaves only, are generally unsatisfactory. Fruits and seeds may or may not be required. Too often collectors carelessly fail to provide the proper equipment for obtaining good specimens, with the result that time is wasted in trying to work with wilted, dried, or otherwise poor material. More detailed directions for collecting are given on page 46.

Implements for Studying Plants.—While the gross morphology of plants can be observed easily, certain fine details, such as the internal structure of the ovary, call for careful dissection. The most useful implements are found in a regular biology dissecting set, but a sharp scalpel or knife, a pair of dissecting needles (which can be made by pushing the heads of coarse sewing needles into the ends of sticks), and a safety-razor blade will suffice. The razor blade is extremely important, for it is often necessary to cut the ovary in longitudinal or cross section to study the ovules and their attachment, and a clean cut with a sharp instrument is best.

A lens also is necessary. A simple hand lens with a magnification of five to ten diameters is generally used by beginners, but a binocular of relatively low power is a great help, especially in work with grasses.

Manuals of Botany.—Many books, large and small, have been written on the plants of different parts of the country. Some of these, like Gray's "New Manual of Botany," cover very large areas; others are for very limited regions. These botanical "manuals" or "floras" concentrate on only a few aspects of botany—generally names and descriptions of families, genera, and

species found in the region, with keys for identification and a glossary of technical terms. Some are illustrated, some are not. They are technical books and are not to be confused with popular books on flowers, since they are for the use of people interested in botany for professional or serious amateur work.

The amateur botanist who has not made a detailed study of floral structure, who has not learned the terminology of plant parts, who has not the patience to make fine distinctions, or whose interest is limited to plants with showy flowers is likely to be discouraged in his first attempts to use technical manuals; but not a few amateurs have overcome these difficulties by hard work and have become quite proficient in identification.

For the use of college students these manuals, more or less local in their range and consequently limited in their content, are of inestimable value, for they provide the most convenient means for the identification of the plants that they are studying.

KEYS FOR IDENTIFICATION

For the beginning botanist analytical keys are almost indispensable, and even the professional often makes use of them.

How Botanical Keys Are Made.—Analytical keys have been used for several generations in books for the identification of plants, and all modern manuals of botany contain them. The principle involved is that of finding contrasting characters and using them for dividing the group being studied into two or more branches. For example, the plant in question and some others may have irregular flowers while some of the group to which they belong have regular flowers. In this way a part of the group is eliminated from the range of possibilities, thus narrowing the problem. Then the key may show that some have simple leaves and others compound leaves and that some are pubescent while others are glabrous. By contrasting a sufficient number of characters, each time eliminating some members of the group, the number of possibilities is finally reduced to one—the name sought for.

In identifying angiosperms it is common practice to have the key first indicate whether the specimen in question is a dicotyledon or a monocotyledon and then by a contrasting series of characters run it down to its family. Another key will similarly direct the search to the genus and a final one to the species. A

natural procedure would be to have keys from the classes to the orders and others from the orders to the families, but most of the manuals omit orders from their keys.

The Structure of Keys.—Several different types of key have been devised for plant identification, two of which are especially important. Both are distinguished by the method of printing them in the book or other publication where they are used.

The *indented* key is the one most used in manuals for the identification of spermatophytes. In this type of key the description of each character is indented a fixed distance from the left-hand margin of the page, the contrasting characters having the same indentation. As progress is made in running a plant through the key, the lines are more and more indented for each pair or group of characters, so that in a large key the lines become very short.

In the *bracket* or *parallel* type of key two or more contrasting characters are described in *consecutive* lines of the page so that they are easily compared. At the end of each line is either the name sought for or a number that, repeated at the beginning of a lower line, carries the search to another contrasting pair or set of characters. This process is continued to the end of the key. For very large keys the bracket form is more suitable than the indented key.[1] The same material arranged in the form of indented keys and of bracketed keys of small size is given for comparison.

INDENTED KEY TO THE FAMILY POMACEAE[2]

Ripe carpels papery or leathery
    Leaves pinnate.. **Sorbus**
    Leaves simple, entire, toothed, or lobed
        Cavities of the ovary (carpels) as many as the styles
            Flesh of the pome with grit cells.................... **Pyrus**
            Flesh of the pome without grit cells
                Cymes simple; trees............................ **Malus**
                Cymes compound; low shrubs.................... **Aronia**
        Cavities of the ovary becoming twice as many as the styles **Amelanchier**

[1] For a very large bracket key see Gilbert M. Smith, "Fresh-water Algae of the United States," 1st ed., pp. 626–644, McGraw-Hill Book Company, Inc., 1933.

[2] BRITTON, N. L., and ADDISON BROWN, "Illustrated Flora of the Northern States and Canada," 1st ed., Vol. II, p. 238, Charles Scribner's Sons, 1897.

Ripe carpels bony
  Ovule 1 in each carpel, or if 2, dissimilar.............. **Crataegus**
  Ovules 2 in each carpel, alike........................ **Cotoneaster**

BRACKET OR PARALLEL KEY TO THE FAMILY POMACEAE

1. Ripe carpels papery or leathery..............................2
1. Ripe carpels bony...6
  2. Leaves pinnate.................................. **Sorbus**
  2. Leaves simple, entire, toothed, or lobed...................3
3. Cavities of the ovary (carpels) as many as the styles..........4
3. Cavities of the ovary becoming twice as many as the styles **Amelanchier**
  4. Flesh of the pome with grit cells.................. **Pyrus**
  4. Flesh of the pome without grit cells........................5
5. Cymes simple; trees............................... **Malus**
5. Cymes compound; low shrubs......................... **Aronia**
  6. Ovule 1 in each carpel, or if 2, dissimilar.......... **Crataegus**
  6. Ovules 2 in each carpel, alike.................... **Cotoneaster**

INDENTED KEY TO THE FAMILY LEGUMINOSAE[1]

Stamens 10, wholly distinct
  Leaves digitately 3-foliolate; flowers yellow............. **Thermopsis**
  Leaves odd-pinnate; flowers white....................... **Sophora**
Stamens (some or all) united by their filaments, at least at base
  Anthers 2 forms; stamens monadelphous................. **Lupinus**
  Anthers all alike, reniform
    Leaves odd-pinnate, without tendrils
      Pod not a loment, 2-valved or indehiscent
        Foliage not glandular-dotted
          Digitately 3-foliolate or rarely 5-foliolate
            Leaflets entire............................ **Lotus**
            Leaflets serrulate or denticulate
              Flowers in racemes...................... **Melilotus**
              Flowers capitate or in short loose spikes
                Pods curved or coiled.................. **Medicago**
                Pods straight, membranous............. **Trifolium**
          Pinnately 5- or more-foliolate (rarely simple or 3-foliolate in *Astragalus*)
            Shrubs.................................... **Robinia**
            Herbs, or rarely with ligneous base
              Keel of the corolla blunt.................. **Astragalus**
              Keel of the corolla acute.................. **Aragallus**
        Foliage glandular-dotted
          Pod with hooked prickles...................... **Glycyrrhiza**
          Pod not prickly
            Shrubs.................................... **Amorpha**

[1] COULTER, JOHN M., and AVEN NELSON, "New Manual of Botany," p. 270, American Book Company, 1937.

Herbs, or merely with ligneous base
    Leaves digitately 3-5-foliolate.............. **Psoralea**
    Leaves pinnately 5-many-foliolate
        Stamens 10.......................... **Parosela**
        Stamens 5........................... **Petalostemon**
  Pod a loment, with reticulated indehiscent joints..... **Hedysarum**
Leaves even-pinnate, terminated by a tendril or bristle
  Style slender, with a tuft of hair near the apex...... **Vicia**
  Style flattened, hairy on the inner side............. **Lathyrus**

Some indented keys, especially very large ones, have numbers, letters, stars, or other characters at the left to make the key easier to follow. This is made necessary by the number of different indentations required, which may even result in one of a pair appearing on one page of the book and its mate on a later page.

BRACKET OR PARALLEL KEY TO THE FAMILY LEGUMINOSAE

1. Stamens 10, wholly distinct.................................2
1. Stamens (some or all) united by their filaments, at least at base.................................3
    2. Leaves digitately 3-foliolate; flowers yellow......... **Thermopsis**
    2. Leaves odd-pinnate; flowers white................. **Sophora**
3. Anthers of 2 forms; stamens monadelphous............ **Lupinus**
3. Anthers all alike, reniform.................................4
    4. Leaves odd-pinnate, without tendrils.........................5
    4. Leaves even-pinnate, terminated by a tendril or bristle.................................17
5. Pod a loment, with reticulated indehiscent joints....... **Hedysarum**
5. Pod not a loment, 2-valved or indehiscent....................6
    6. Foliage not glandular-dotted...............................7
    6. Foliage glandular-dotted...................................13
7. Digitately 3-foliolate or rarely 5-foliolate....................8
7. Pinnately 5- or more-foliolate (rarely simple or 3-foliolate in *Astragalus*).................................11
    8. Leaflets entire.............................. **Lotus**
    8. Leaflets serrulate or denticulate............................9
9. Flowers in racemes.............................. **Melilotus**
9. Flowers capitate or in short loose spikes...................10
    10. Pods curved or coiled......................... **Medicago**
    10. Pods straight, membranous.................... **Trifolium**
11. Shrubs... **Robinia**
11. Herbs, or rarely with ligneous base........................12
    12. Keel of the corolla blunt..................... **Astragalus**
    12. Keel of the corolla acute..................... **Aragallus**
13. Pod with hooked prickles.......................... **Glycyrrhiza**

13. Pod not prickly 14
    14. Shrubs .... **Amorpha**
    14. Herbs, or merely with ligneous base 15
15. Leaves digitately 3-5-foliolate .... **Psoralea**
15. Leaves pinnately 5-many-foliolate 16
    16. Stamens 10 .... **Parosela**
    16. Stamens 5 .... **Petalostemon**
17. Styles slender, with a tuft of hair near the apex .... **Vicia**
17. Style flattened, hairy on the inner side .... **Lathyrus**

Keying Large versus Small Groups.—The making and using of a key for a small group is obviously much easier than for a large group. A key to all the families of angiosperms in the United States would have to make use of many distinctions, some of them based on rather fine points, but a key that included only the families of a small area would call for the use of only a few easily determined characters.

TROUBLESOME VARIATIONS AND EXCEPTIONS

Both in the use of keys and in comparing with descriptions, some allowance has to be made for exceptions and for variations in individuals, or even in the parts of an individual.

Intergrading Characters.—To contrast the characters, as is done in keys, they need to be clear-cut and distinct. If they intergrade, the student is often perplexed to know where the line should be drawn and which branch to follow in the key. If one has to contrast blue flowers with red flowers and those of his specimen are purple, or if the key contrasts pubescent leaves with glabrous leaves and his specimen bears a few scattered hairs, he is in doubt which branch of the key his specimen fits best. Some keys are much better constructed than others in this respect and avoid intergrading characters. When there is doubt which branch of a key to follow, it often becomes necessary to follow one until the correct goal is reached or until there is evidence that one is working in the wrong section of the key, and then, if necessary, to go back and follow the other. Theoretically this should never be necessary, but practically it sometimes is.

Exceptions to Rules.—Some individuals and some species do not fit in all respects the descriptions laid down for the groups in which they are found. Some hawthorn shrubs bear few or no thorns. Lupines are generally blue-flowered, but some are white or nearly so; in fact, albino flowers are not uncommon in various

shows leaves from the same individual plant of mountain maple varying from simple and nearly entire to compound. In some species, *e.g.*, *Thlaspi arvense*, the lower leaves are petiolate and the upper ones are sessile and clasping. Great variation can be found in the size of flowers in some species. Species with most members erect may have some individuals that are prostrate or nearly so, and vice versa. The habitat in which the plants are growing may affect their morphology considerably, especially the size. It will be remembered, however, that environmental conditions, such as moisture and light, affect the leaves and stems much more than the flowers.

Considerable experience, judgment, and patience are required to know how much deviation may be allowed from the key or the description.

Fruits and Seeds.—A good, full description of a group such as a genus or a family will include the fruits and perhaps also the seeds. However, it is often annoying to find such characters in keys, because the specimen being identified, although it has good flowers, may be too young to have well-developed fruits. This difficulty is most commonly met with by classes that run during the second semester or the spring quarter of the college year. Fortunately, a careful study of the ovaries will enable the student to anticipate some of the fruit and seed characters, such as the number of seed chambers and seeds and where the seeds are attached, *i.e.*, the placentation. It has been found especially difficult to avoid using fruit characters in making generic keys to certain families, notably Cruciferae and Umbelliferae.

Comparing with Descriptions.—A serious mistake commonly made by beginners is to assume when a category is reached—*e.g.*, family or genus—that there has been no mistake in observation or interpretation and that the correct group has been found. An error may lead to endless trouble, and the student should make it an *invariable rule* to compare the specimen with the description of the group before he starts to run it down to a lower category. Not infrequently he will thus find that the plant does not fit the description in one or more important characters because he has made an error and placed the plant in the wrong group.

PORTRAYAL OF PLANTS AND PLANT GROUPS

In order to discuss individual plants, species, and larger groups

scribing them, for names are insufficient except among people who are very familiar with what the names stand for. While showing the plants under consideration is most effective, it is often impracticable because they are not available at the time. Several methods are in common use for describing plants, all of which are useful but none perfect.

Descriptions in Common Terms.—It is surprising how difficult it is to describe a plant in simple language so that another person familiar with it will recognize it. In fact, it may be said that, except for a few kinds of plants with very unusual characters, such as pines, oaks bearing acorns, insect-catching plants, and water-lilies, attempts to identify plants by such descriptions usually fail.

Descriptions in Technical Terms.—The use of technical terms ensures brevity, for in common language a whole sentence or more may be required to state what is covered by a single technical word such as "spadix" or "ament." Technical descriptions have been written for all named species and for the higher categories. A botanist reading such a description can often visualize the appearance of the plants in question sufficiently to identify them. If the description is written, it will be accompanied by the name; but even if it is given verbally without the name, the description will often bring recognition. Such a description will be meaningless, however, to the layman.

Illustrations.—These may be photographs, drawings, or paintings. For individual plants and for species, coloration is helpful but expensive. Photographs and paintings show only the large, general features and do not bring out details of stamens and pistils or internal anatomy. These may, however, be shown in fine, detailed drawings. Illustrations are used mostly to supplement worded descriptions. Drawing of flowers or entire plants by students in the laboratory has been largely abandoned because of the time required and the inability of most students to produce good results.

Floral Diagrams.—Many years ago the happy idea was conceived of representing the essential features of floral morphology by rather simple diagrams of cross sections, more rarely longitudinal sections, of the flower. In this way such characters as numbers and union of parts, symmetry, and most others can be represented by a person who is not an artist and in much less time than is required for perspective drawings, although these dia-

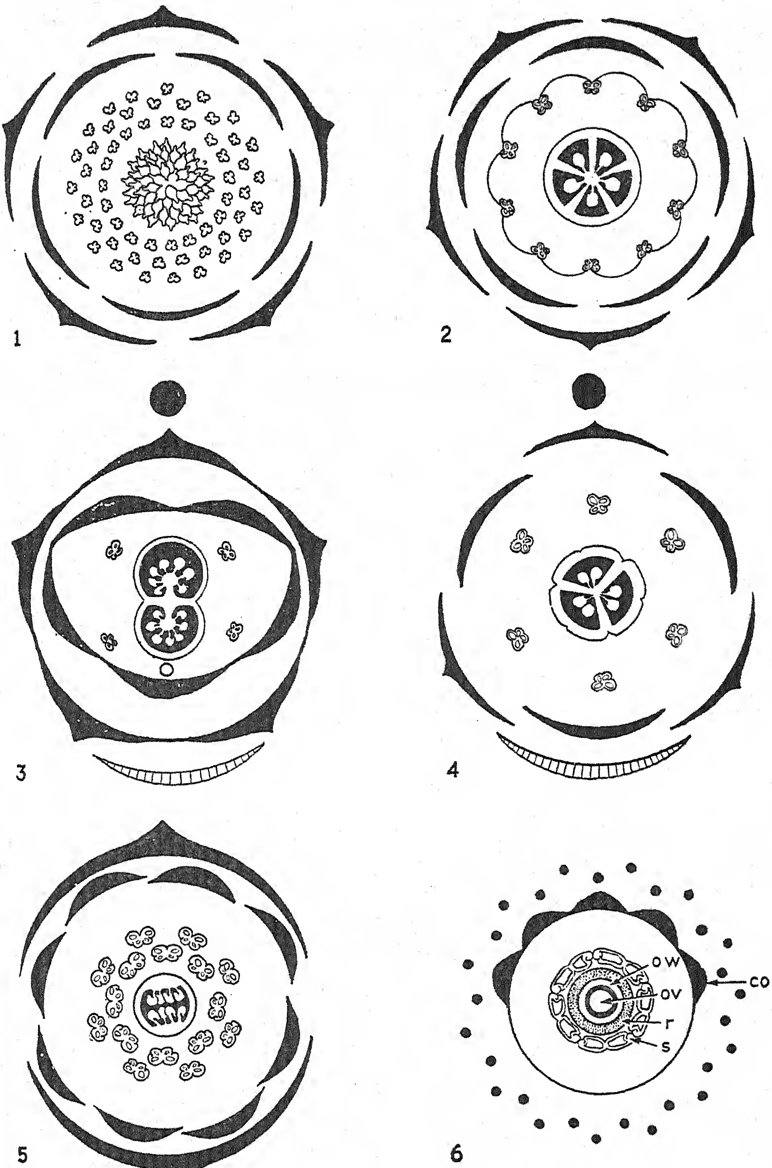


FIG. 5.—Representative floral diagrams. 1, 2, 5, and 6 are terminal flowers; 3 and 4 are axillary—the stem is represented by the black dot above and the leaf in the axil of which the flower is borne is shown below. 1, *Ranunculus*. 2, *Geranium*. 3, *Pentstemon* (irregular). 4. *Lilium*. 5 *Sanguinaria*. 6

grams are not rated as beautiful. Some institutions make use of this method of description in the laboratories, others do not. It is worthy of more general application than it receives.

Floral Symbols and Formulae.—Some years ago Dr. F. E. Clements proposed a method of describing species and larger categories of flowering plants that has found favor with many botanists. Morphological characters such as calyx, pistils, and stamens are represented by suggestive letters (CA, P, and S), the number of each being indicated by figures. A few other distinguishing marks are used also. These are the "symbols," and combinations of them make up the "formula," which stands for a definite species, genus, family, or order.

The system seems at first somewhat complicated, but the symbols required are rather few, generally suggested by the letters used, and therefore easily learned. With a little practice the student can describe a species more quickly by this method than by any other. Formulae for families offer a little more difficulty because of the fact that the members composing them are not all alike and it may be hard to provide for exceptions. For example, nearly all of the Cruciferae have four petals, Co^4, but *Lepidium apetalum* has none, Co^0. The symbol Co^{0-4} could be used, but this might give the impression that an apetalous condition in the flowers of Cruciferae is more common than it really is. Likewise, orders, which have even greater diversity of species than families, are still more difficult to represent by formulae, although it can be done[1] if a little allowance is made for unusual species in the order.

THE FLORAL CHART

Clements also devised a floral chart to amplify the Besseyan conception of the flowering plants. As he first depicted it, and as later modified by other taxonomists, it serves both as a key to families or orders and as a graphic representation of relationships.

Across the branching phylogenetic system of Bessey, lines are drawn irregularly from left to right, each representing an important character. For example, all families or orders below a certain line have regular corollas, while those above it have irregular corollas. All below another line have carpels distinct, while all above it have them united. By noting that these lines cross the

[1] See Raymond J. Pool, "Flowers and Flowering Plants," 2d ed., chart opposite p. 159, McGraw-Hill Book Company, Inc., 1941.

KEY TO FLORAL SYMBOLS AND FORMULAE

CA Calyx, sepals

Co Corolla, petals

Coz Corolla zygomorphic

Sc Scales

S Stamens

P Pistils

0 None

$1-5$ One to five

$2+3$ Organs in two sets

x Few, variable

∞ Many, variable

$\bigcirc$, $\boxed{}$ United

$\frown$ United above

$\smile$ United at base

$(\quad)$ The exceptional condition

CA^{x} Sepals several

CA^{P} Calyx a pappus

Co^{0} Apetalous

$\mathrm{Co}^{\underset{\smile}{4-6}}$ Petals 4–6 united at base

$\mathrm{Co}^{\textcircled{5}}$ Corolla of 5 united petals

S^{∞} Stamens many

$\mathrm{S}^{\underset{\smile}{5}}$ Stamens 5, filaments united

$\mathrm{S}^{\widehat{10}}$ Stamens 10, anthers united

S^{2+4} Stamens 6, in two sets

$\dfrac{\mathrm{S}}{\mathrm{Co}}$ Stamens epipetalous

$\mathrm{CA}^{3}\mathrm{Co}^{3}\mathrm{S}^{6}\mathrm{P}^{\textcircled{3}}$

Complete flower, 4 sets of floral parts attached to receptacle

$\mathrm{CA}^{0}\mathrm{Co}^{0}\mathrm{Sc}^{2-4}\mathrm{S}^{3}\mathrm{P}^{\boxed{1:3}}$

Incomplete flower, scales 2-4, ovary one-celled but tricarpellate

$\mathrm{CA}^{5}\mathrm{Coz}^{\underset{\smile}{2}+\underset{\smile}{2}+1}\mathrm{S}^{\underset{\smile}{9}+1}\mathrm{P}^{1}$

Corolla zygomorphic with 3 sets of petals; stamens in 2 sets, 9 united by their filaments

$$\frac{\mathrm{S}^{5}}{\mathrm{CA}^{5}\mathrm{Co}^{\textcircled{5}}\mathrm{P}^{\textcircled{2}}}$$

Stamens epipetalous, pistil bicarpellate

$\mathrm{CA}^{5}\mathrm{Co}^{0-5}\mathrm{S}^{5}$ or $\mathrm{CA}^{5}\mathrm{Co}^{0}\mathrm{P}^{\textcircled{5}}$

Imperfect flowers, either staminate or pistillate

$$\frac{\mathrm{CA}^{5}\mathrm{Co}^{5}\mathrm{S}^{5-10}}{\mathrm{P}^{\textcircled{5}}((\boxed{1:3-5}))}$$

Ovary inferior, usually five carpellate but rarely with one cell and 3-5 carpels

$\overline{\mathrm{P}}$ Epigynous, inferior

P^{∞} Pistils many, unicarpellate

$\mathrm{P}^{\underset{\smile}{5}}$ Carpels 5, united at base

$\mathrm{P}^{\textcircled{3}}$ Pistil one, tricarpellate

$\mathrm{P}^{\boxed{1:3}}$ Pistil one celled, tricarpellate

$\mathrm{P}^{\textcircled{3}}((\boxed{1:6}))$ Pistil tricarpellate, rarely one-celled with 6 carpels

$$\frac{\mathrm{CA}^{\mathrm{P}}\mathrm{Co}^{5}}{\mathrm{P}^{\boxed{1:2}}}$$

Imperfect flower; stamens missing; calyx represented by a pappus; ovary inferior, one celled but bicarpellate

$$\frac{\mathrm{S}^{4-5}}{\mathrm{CA}^{\underset{\smile}{5}}\mathrm{Co}^{\underset{\smile}{5}} \text{ or } \mathrm{Coz}^{\underset{\smile}{5}}} \Big/ \mathrm{P}^{\textcircled{2}}$$

Corolla actinomorphic or zygomorphic; stamens epipetalous; ovary inferior

$$\frac{\mathrm{CA}^{3}\mathrm{Co}^{0}\mathrm{S}^{3-0}}{\mathrm{P}^{\textcircled{2}-0}}$$

Flowers perfect or imperfect, apetalous

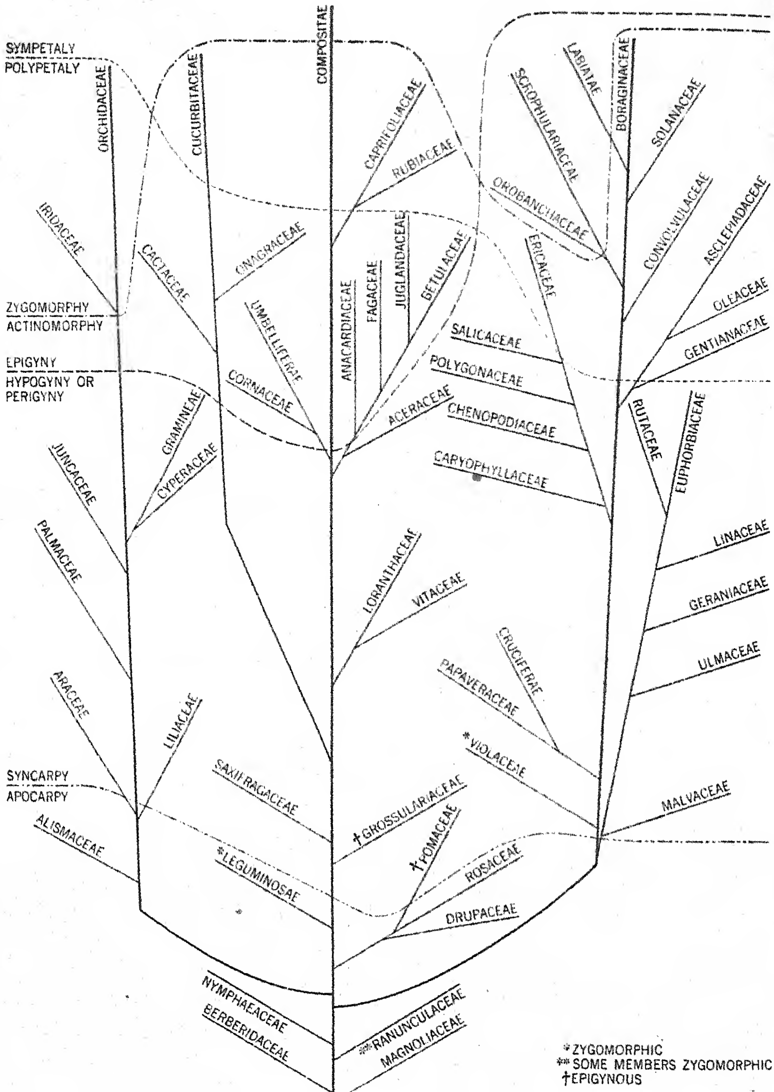


FIG. 6.—Floral chart of the families of Angiosperms discussed in this book arranged essentially according to the system of Bessey. The left-hand branch represents the Monocotyledons and the other two main branches the Dicotyledons. The broken cross lines show that the same evolutionary phenomena have occurred repeatedly in different groups of higher plants. Important exceptions are recorded in notes in the lower right-hand corner, but occasional species showing deviations from the rules occur in many other families.

several branches of the phylogenetic system, it is seen that the same evolutionary changes, *e.g.*, irregularity of flowers, union of carpels, and unisexuality, took place repeatedly in different phylogenetic lines and at different times, as processes distinct from each other.

Floral charts have been made for both families and orders and are convenient instruments for keying plants to their groups. Charts for orders are simpler to follow than those for families, because there are fewer orders than families in the class Angiospermae, but they are usually of less value, since most manuals have keys for tracing members of the families to genera but few or none for tracing members of orders to families. Therefore, tracing the plants to the order by means of the chart does not aid in the identification.

Floral charts, like keys, are easier to make and easier to use if small, with few families, than if large, with many families. Such a chart, constructed to include all the angiosperm families of the entire world, would be too extensive for pages the size of an ordinary textbook, although it could be placed on a large wall chart. If this method of portrayal becomes generally popular, manuals may adopt it for the families found in the limited area covered by the book.

The example given on page 42 makes no pretense of completeness for the entire United States but includes most of the large and important families and will serve to illustrate the principles included.

A difficulty arises when the members of a group vary with respect to a character used as the basis for a cross line. This is illustrated especially well by irregularity of flowers. In the order Rosales most of the families have regular flowers, but those of Leguminosae are irregular. In Ranunculaceae the flowers of *Ranunculus* and *Anemone* are regular, while those of *Delphinium* and *Aconitum* are irregular. It may be that with experience such characters will not be used as a basis for cross lines, or possibly orders and families will be subdivided on the basis of these characters, although this alternative seems hardly likely.

THE WORK OF SPECIALISTS

A number of large or difficult genera, *e.g.*, *Senecio*, *Carex*, *Pentstemon*, *Lupinus*, *Astragalus*, and *Poa*, have been studied

with great thoroughness, each by a different specialist. The purpose of this work is to find where specific lines should be drawn, revise specific descriptions, make ecological studies on the different species of the genus, etc. In carrying on these studies the investigators have traveled much, collected widely, and visited different institutions to study the specimens in their herbaria. Such specialists have become authorities in their fields and have done much valuable work by identifying specimens sent them and verifying or correcting the names of the specimens in institutional herbaria. While much of their time is given to the service of others, they receive in return the benefit of studying a wide range of specimens.

CHAPTER III

PREPARATION OF HERBARIA

Not until the sixteenth century did botanists make any systematic attempt to preserve for future reference the specimens they studied. Prior to that time a few dried herbs intended primarily as a supply for medicinal purposes served occasionally as comparative material.

About 1550, Cesalpini and his Italian associates and a few central European botanists began quite definitely to preserve some of the material they studied. The wisdom of this procedure was soon appreciated by others and herbarium making became a great feature of botanical work. In every civilized country today plant collections of untold value can be found. Probably the greatest is at the Royal Botanic Gardens, Kew, England, while in America the Gray Herbarium at Harvard University and the collections in the National Museum, Washington, D.C., the New York Botanical Garden, and the Missouri Botanical Garden are outstanding.

Purposes of Herbaria.—Words are but poor instruments for describing plants. The best description leaves much about the plant unsaid. Many pages would be required to describe a pine tree completely, but species are so numerous that their descriptions must be brief. Furthermore, the different individuals of a species vary somewhat. No two are exactly alike. A specific description, then, is but an approximation. Often the botanist who describes a species is unduly impressed by certain features, especially conspicuous on certain individuals, while he overlooks, minimizes, or ignores other features. As a result other botanists find the specific description unsatisfactory or difficult to apply. Even drawings and photographs fall far short of what is desired in showing individual variation and details of structure and development. In very many cases it is necessary to compare descriptions with actual specimens, many in number and from widely separated regions. This work is of the greatest importance and has

resulted in better descriptions and in the dividing and uniting of groups along more nearly correct lines. To do this revision in the field is usually considered impracticable because time there is too valuable, suitable equipment is not available, and weather conditions are sometimes unfavorable. Furthermore, it is less expensive to ship specimens to a few central points where they can be examined than to travel over the world to study them where they grow. As a result of centuries of experience most comparative studies for taxonomic purposes are made in the herbarium and the laboratory. The man who works indoors too exclusively, however, has a narrowness of view that is likely to be evident in his writings. Sometimes, indeed, laboratory and herbarium distinctions must be repudiated because of field observations, as when specimens taken from different branches of the same tree and studied separately have been given different specific names.

The working herbarium of today is much used for comparison with new material. Botany is becoming more and more popularized and applied, and in many sections of the country much material of an economic nature is sent to state authorities for examination and report. This material is often fragmentary, lacking reproductive parts, and poorly preserved. It would require a highly experienced systematist to identify it at sight or with books alone, but the average botanist with known specimens for comparison can determine most of it quite readily.

Preserved specimens are also much used to show visitors, both professional and unprofessional, and have become important as a means of technical and liberal education.

Methods of Collecting.—A satisfactory series in any given species will include specimens in every stage of growth and reproduction and from different localities and habitats. The most satisfactory single specimen, if only one were available, would be in the late flowering stage, showing both flowers and young fruits, and collected from a normal habitat, but a considerable number of plants are required to tell the full story of a species in all its varying aspects.

A complete specimen includes all parts of the plant, even the root. It is impracticable to collect unbroken root systems, however. Furthermore, most specific descriptions do not mention the roots at all. In some cases, however, roots and other underground parts are necessary for identification. An experienced

collector will know which groups require underground portions and which do not and will be governed accordingly. The beginner should in every case collect enough of the root system of an herbaceous plant to show its general character.

For taxonomic purposes the specimens should be selected to represent the species rather than to suit the fancy of the collector. If few in number, they should be of usual rather than unusual

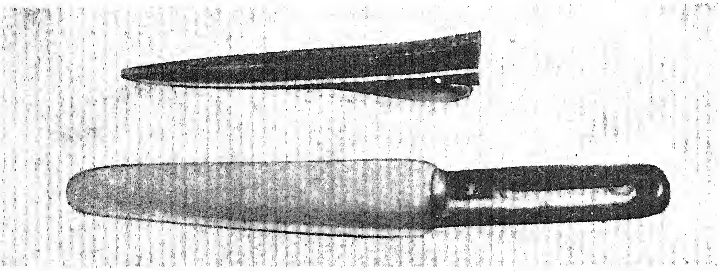


Fig. 7.—Trowel for securing underground portions of herbaceous plants. Such an instrument must be heavy and strong and made of good steel.

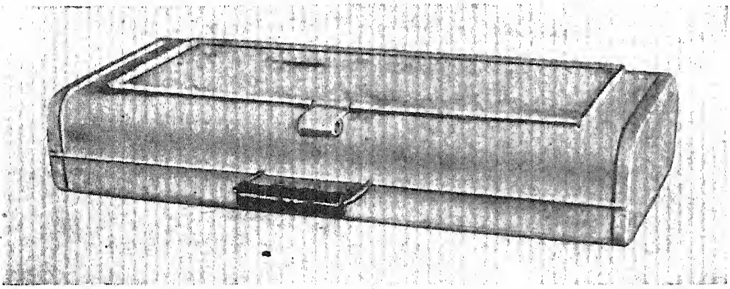


Fig. 8.—Vasculum for collecting plants. It can be made of tin or of light galvanized iron and in any dimensions.

types. If many specimens are available, they should include all types. On account of the limited size of the sheets of mounting paper there is a temptation to select small individuals when large kinds of plants are being collected, but this must not be overdone.

METHODS OF PRESERVATION

On account of the bulky nature of plants it has long been the custom to press them flat. Admittedly this distorts their shape, but it has been found to be the only practical method for use on a large scale. To produce good herbarium specimens the plants must be pressed before they wilt. The difficulty in doing this is

so great that wrinkled specimens are frequent in many collections. A common method is to collect in a tin vasculum and press immediately on return from the day's trip. With care good results may be had in this way. Generally it is not advisable to wet the plants to delay wilting or to restore turgidity, since this increases the tendency to discolor in the press, although the use of a wet paper lining in the vasculum is free from this objection. The finest preservation can be secured by the use of a field press in which the plants may be placed as soon as gathered. For collecting in open country the automobile has become a convenience, but much important work must be done in places inaccessible to it.

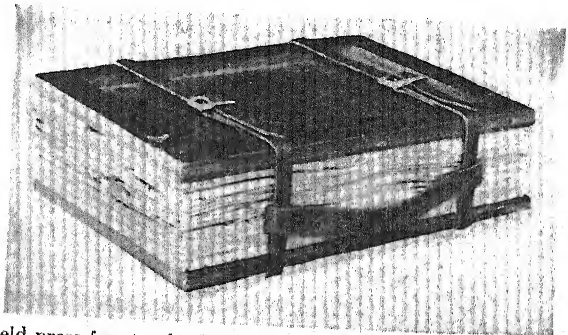


FIG. 9.—Field press for standard-sized driers. The pressure is obtained by the use of straps.

Methods of Pressing.—A rather standard procedure is followed in pressing plants. They are laid between sheets of newspaper, or plain inner sheets of similar quality, which are alternated between driers of heavy absorbent blotting paper and the whole covered with a board and weight. For use in a field press when traveling, ordinary press boards are too heavy, and slatted frames of wood, thin veneer board, or strong cast aluminum are much to be preferred. In place of a weight the field press is held by straps or clamps. Drying is obtained chiefly by transfer of moisture from the plants into the blotters, and to get good contact and prevent wrinkling the weight should be as heavy as possible without crushing the plant tissue.

Difficulty is found in building up a press full of plants to a thickness of several inches. Since the plants are laid mostly in the middle of the paper folders and may or may not extend to the

edges, greater pressure is applied to the center than to the margins, which are more or less empty. The author has devised press boards of thin plywood or composition material, such as "tempered presdwood," with wooden strips ½ to ¾ inch in thickness along the sides. Pressure of straps or weights on these strips forces a bend in the boards and increases the pressure on the plants at the margins, thus preventing their shriveling in drying.

To prevent discoloration and molding, the driers (but not the inner sheets) must be changed. The number and frequency of changes will depend on the character of the plants and the dryness of the climate. Changing every day for two or three days and

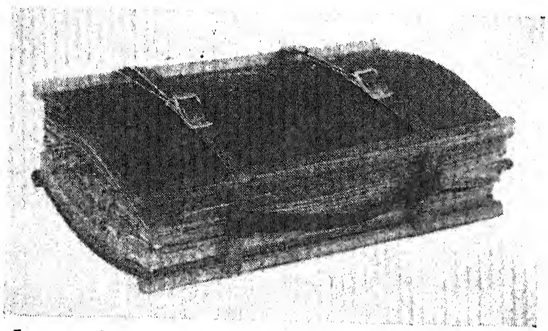


FIG. 10.—Improved plant press. The strips along the sides of the flexible boards give increased pressure at the margins where there is less plant material. This prevents the shriveling that occurs at the margins in the ordinary plant presses.

then two or three more times at longer intervals is a good rule, but this is excessive for most plants in an arid region. Considerable judgment and a methodical system are required to secure good specimens with a minimum amount of labor. If the plants are fairly uniform in moisture content, all can be kept together and the driers changed at the same time. If some, like grasses, are relatively small and dry while others are thick and succulent, they can best be segregated, either when they are put into press or when the driers are changed the first time. The succulent ones will require changing more frequently and long after the others are safely dry.

It is very difficult to dry some kinds of plants without their blackening. Saprophytes without chlorophyll, such as Indian-pipe, succulent hydrophytes, and plants wet with rain or dew give

the greatest difficulty, and they must be treated accordingly. Experience has shown that some species discolor more than others of similar texture. Plants such as those just mentioned should have the driers changed two or three times a day for several days. The superior quality of the product amply justifies the additional work. Even this care will not completely prevent discoloration of some species.

Use of Artificial Heat.—Under some circumstances it is desirable to use artificial heat to facilitate drying. This method is especially useful in very damp climates, when making extensive collections while moving rapidly from place to place, and when pressing specimens that are known to give trouble by blackening.

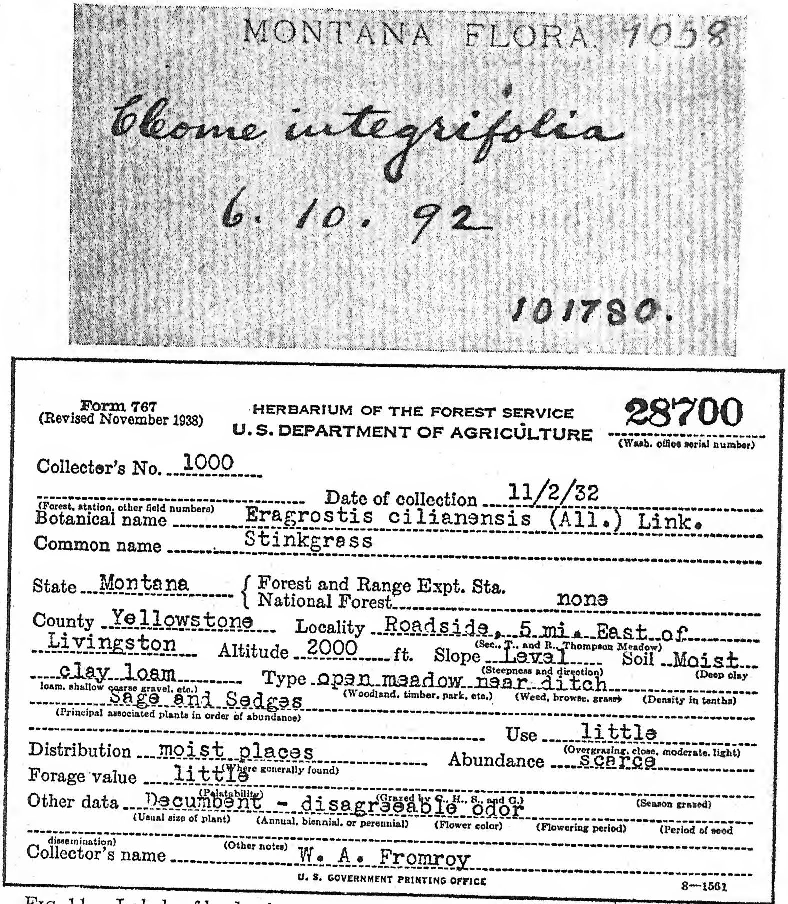
The method is as follows: The specimens are pressed in the usual way for a few hours until wilted. Sheets of corrugated cardboard, smooth on both faces, or of aluminum with fine cross corrugations, are then put between the driers. Some prefer to omit the driers if cardboard is used. The press is then strapped together again and hot air is forced through the corrugations. The best source of heat is an electric hot plate or toaster, since an oil heater or other open flame gives off moisture of combustion. Specially constructed, ventilated boxes with light bulbs in the bottom are recommended.

The heat does not readily pass through the narrow corrugations but has to be forced through. At least three ways are used to accomplish this: (1) The press may be set edgewise over the source of heat, with the corrugations vertical, and surrounded by a canvas skirt to direct the hot air upward through the press. (2) The press may be put in an oven the heat of which is automatically controlled, and a small electric fan placed in the oven with it to force the warm air through. This is the best method for indoor work. (3) When an automobile is used in collecting, the press may be placed on the fender beside the hood in such a position that the heat from the engine is forced through the press. Most of the newer types of car do not give off heat from the sides of the hood, but the warm air of summer forced through by the motion of the car serves very well. In fair weather this method is highly successful.

Small or rare specimens may be dried quickly with an electric iron, the plants being placed between layers of heavy cloth or paper. Drying by artificial heat is a rapid method, and after 6 to

12 hours the plants are usually ready to be transferred to an ordinary press and finished with regular blotters.

Mounting of Specimens.—When dry, the plants are mounted on sheets of heavy white paper to support them in handling. The



MONTANA FLORA 7058

Cleome integrifolia

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Form 767 (Revised November 1938)

HERBARIUM OF THE FOREST SERVICE
U. S. DEPARTMENT OF AGRICULTURE

28700 (Wash. office serial number)

Collector's No. 1000

(Forest, station, other field numbers) Date of collection 11/2/32

Botanical name Eragrostis cilianensis (All.) Link.

Common name Stinkgrass

State Montana { Forest and Range Expt. Sta. National Forest none

County Yellowstone Locality Roadside, 5 mi. East of Livingston (Sec., T., and R., Thompson Meadow) Altitude 2000 ft. Slope Level (Steepness and direction) Soil Moist clay loam (Deep clay loam, shallow coarse gravel, etc.) Type open meadow near ditch (Woodland, timber, park, etc.) (Weed, browse, grass) (Density in tenths)

Sage and Sedges (Principal associated plants in order of abundance)

Use little (Overgrazing, close, moderate, light)

Distribution moist places (Where generally found) Abundance scarce

Forage value little (Palatability) (Grazed by C., H., S., and G.) (Season grazed)

Other data Decumbent - disagreeable odor (Usual size of plant) (Annual, biennial, or perennial) (Flower color) (Flowering period) (Period of seed dissemination) (Other notes)

Collector's name W. A. Fromroy

U. S. GOVERNMENT PRINTING OFFICE 8—1561

FIG. 11.—Labels of herbarium specimens. Upper, a poor label with inadequate data. Lower, the label used in the extensive collections of the U.S. Forest Service. It contains more ecological data than do most herbarium labels.

standard sheet in this country is $11\frac{1}{2}$ by $16\frac{1}{2}$ inches. The plants are fastened to the sheets by glue or gummed cloth strips or both. The amateur should mount only one plant on a sheet no matter how small it is or how many, presumably of the same species, are to be mounted. Failure to follow this plan has

frequently resulted in plants of two or more species, superficially resembling each other, being mounted on the same sheet. However, professional botanists who are authorities on the species often mount several specimens on a sheet. The label is preferably attached to the lower right-hand corner. It is a great mistake to mount plants on paper of a quality that will become yellow or brittle with age. This is a poor way to economize.

Storage.—In large institutional herbaria the mounted plants are usually kept in specially constructed herbarium cases. Steel is necessary for safety, since many herbaria have been destroyed by fire to the despair of their owners. The arrangement of specimens in the cases is partly a matter of convenience. Usually the families are arranged according to a well-known taxonomic system, most commonly that of Engler and Prantl, or, less frequently, that of Bessey, or sometimes a modification of one of these. Within the families, however, the genera are often arranged alphabetically, and within the genera an alphabetical arrangement of species is still more common. Subgenera are usually ignored in the labeling of specimens and in their arrangement in the herbarium cases.

In damp climates especially, it is necessary to avoid basement storage for herbarium specimens on account of mold. More often, particularly in the south, the specimens are likely to be damaged by insects, some kinds of which eat the gum of the labels, others the pollen or other parts of the plants themselves. Four methods are in use to prevent insect depredations: (1) Poisoning of the specimens by dipping them in a 2 per cent solution of mercuric chloride in a mixture made by adding one part of petroleum ether to two parts of 95 per cent alcohol. The specimens dry quickly between blotters under light pressure. The method is obviously unsatisfactory for specimens that have already been mounted on paper. (2) The use of chemicals that act as repellents to the insects. Of these, moth balls and naphthalene flakes have been much used in herbarium cases. More effective is a mixture of one part of paradichlorobenzene (dichloricide) to five parts of naphthalene, kept in the cases and renewed once a year. They keep the insects away but do not kill them. (3) The application of insecticidal fumigants. Of these carbon bisulfide has been most used. It can be placed in dishes or trays in the top compartments of the herbarium cases, and, being a

volatile liquid, it will diffuse downward among the plants. For the fumigation of small herbaria, transferring from the cases to a tight sheet-metal box containing the fumigant and leaving overnight is sometimes preferred. Carbon bisulfide has a disagreeable odor and it is highly inflammable, making it dangerous for use in a room with an open flame. Furthermore, its insecticidal value is not as high as was once supposed. For these reasons it is being replaced by a mixture of ethylene dichloride three parts and carbon tetrachloride one part, which is extensively used in flour mills, is easily obtainable, and is not inflammable. (4) The use of heat. Insects are killed by heat at a relatively low temperature.[1] The plants are placed on shelves in an electrically heated steel case with a dish of water. Four to six hours at 60°C. has been found to kill all troublesome insects and their eggs.

The Preservation of Type Specimens.—Type specimens are so valuable that they should be preserved with especial care. Pressed plants are extremely fragile and repeated handling, even though carefully done, will inevitably result in more or less damage. In many herbaria they are kept apart from the regular specimens in separate steel cases, and in recent years there is a tendency to keep each one in a separate cellophane envelope. Most herbarium curators will not permit them to be shipped for examination.

Labeling and Field Data.—The minimum of information to place on each sheet is the botanical name of the specimen, the locality as definitely as possible—at least stating the county or even the township—the date of collection, and the name of the collector. It is most unfortunate that so many herbarium specimens bear no other data. Ecologists are now doing splendid work in showing the effects of habitat on morphology and also the distribution of species and subspecies according to habitat, and their work would be made much easier if all preserved specimens available to them bore data concerning soil, moisture, altitude, exposure, associated species, etc. There is not the slightest doubt that many individuals of the same species are masquerading under different names because of modifications produced by environment.

[1] See Hugh O'Neill, Heat as an Insecticide in the Herbarium, *Rhodora*, **40**: 1–4, 1938. The design for an electric heating box is given here along with the method.

Two methods for recording field data are used by experienced collectors: (1) A field notebook can be kept in which appear numbers that correspond with specimens collected. The notebook contains much information, the pertinent part of which is later transferred to the herbarium label. (2) Printed forms with headings indicating the desired information can be put up in convenient-sized pads, one being filled out and included with each specimen. These slips are applicable to collections made with a field press but are not so good for plants collected in a vasculum. The field data should apply specifically to the individual plant in question, not simply to the usual habitat in which that species is found.

The herbarium should be looked upon as a working tool, and its quality and condition will be reflected in the results obtained from its use.

CHAPTER IV

THE TERMINOLOGY OF SYSTEMATIC BOTANY

Classification and nomenclature are based chiefly on a detailed knowledge of comparative plant morphology and anatomy. Every part of the plant is studied in its minutest detail and compared with similar structures in other plants. For this reason every organ must have a name, and many adjectives must be used to designate the different forms of the organ. It is natural, therefore, that a formidable array of terms should have come into use—the terminology of systematic botany.

The student can make little progress in naming and classifying plants until he has learned the fundamentals of morphology as they are taught in courses in general botany. To this information he must add a special knowledge of the terms used in describing the floral and vegetative organs. The more important of these are discussed in this chapter and should be mastered.

It should be clearly understood that this chapter is not to be confused with a glossary of botanical terms. A glossary is simply a list of technical terms, with their definitions, arranged alphabetically, with no relationship between each term and those adjacent to it. In this chapter on terminology[1] the morphology of organs or parts is taken up in such a way that comparisons of different forms or types of like parts are easily made, thus emphasizing the meaning of these terms. For example, under "Leaf Margins," *entire* is contrasted with *dentate*, *serrate*, etc., and under "Surface Coverings" *pubescent* is contrasted with *hirsute*, *tomentose*, etc.

No alphabetical glossary is given in this book since the student will always have ready access to glossaries in manuals and in the

[1] Two older books that give botanical terms in classified arrangement, and with illustrations, rather than in alphabetical order are (1) John Lindley, "An Introduction to Botany," 4th ed., Vol. II, pp. 344–383, Longmans, Green and Company, 1848; (2) Asa Gray, "Lessons in Botany," rev. ed., pp. 1–128, American Book Company, 1887. They have served a very useful purpose.

special books cited on page 329. Dictionaries contain practically all such words and their definitions.

The terms are here classified in logical sequence under the following headings:

ROOTS

Roots differ from stems in the absence of nodes and leaves. They branch at irregular intervals and may produce adventitious buds.

Position:

Primary.—Formed by an extension of the radicle of the embyro.

Secondary.—Branching from other roots.

Terrestrial.—Growing in the earth.

Aerial.—Growing in the air.

Adventitious.—Growing from stems or leaves.

Prop.—Growing from the stem above ground and entering the soil for mechanical support.

Morphology:

Tap.—A main root growing straight downward.

Fascicled.—Arranged in a cluster and approximately equal in size.

Fibrous.—Slender and usually tough.

Fleshy.—Relatively thick in diameter from the presence of stored food.

STEMS

Stems produce nodes at more or less regular intervals, with internodes between. Each node normally bears one or more leaves with a bud in the axil. When these buds form branches, the branches are classed as parts of the stem. Stems may be so specialized that they are not readily recognizable.

Position:

Shoot.—Any portion that has been formed by one growing point. Usually it is relatively straight. The shoot does not include its branches, any one of which may also be called a shoot. The term is also used to designate stem and leaves collectively.

Twig.—A short lateral branch of a woody stem, generally bearing foliage leaves and sometimes flowers.

Decumbent.—Lying prostrate, with the tip turned upward.

Caudex.—The base of an herbaceous perennial that survives after the top has died back at the end of the season.

Shape:

Cylindrical.—Circular in cross section.

Terete.—Same as cylindrical.

Quadrangular.—Square in cross section.

Texture:

Herbaceous.—Dying to the ground at the end of the season's growth.

Woody.—Living over winter and hard in texture.

Shrubby.—Woody, with more than one trunk.

Suffrutescent.—Woody at the base, the upper portion dying back at the end of the season.

Specialized Stems:

Rootstock.—A horizontal, underground stem bearing scale-like leaves and usually shoots and adventitious roots. Its functions are food storage and vegetative propagation.

Rhizome.—Same as rootstock.

Tuber.—A fleshy, underground stem bearing scale-like leaves with buds in their axils. Its function is food storage and vegetative propagation. It differs from a rootstock in being proportionately shorter and thicker.

Corm.—The fleshy, underground base of a stem, usually spherical in shape or broader than high. Its functions are food storage and vegetative propagation.

Bulb.—A rounded, underground structure consisting of a short, basal stem bearing fleshy, scale-like leaves that make up the bulk of the organ. Its functions are food storage and vegetative propagation.

Tendril.—A lateral climbing organ, sometimes stem and sometimes leaf.

Thorn.—A strong, sharp-pointed protective organ containing vestiges of a stele. Most thorns are short lateral branches.

Prickle.—A sharp protective organ that is a lateral extension of the cortex and epidermis.

Cladophyll.—A stem having the appearance and functions of a leaf.

BUDS

Buds are very short stems, usually lateral branches, bearing specialized leaves.

Kinds:

Dormant.—Inactive, usually because of the winter or a dry season.

Leaf.—Those that are the beginnings of shoots and do not contain floral parts.

Flower.—Unopened flowers.

Mixed.—Dormant buds that contain undeveloped foliage leaves with flower buds wrapped up inside them.

Position:

Terminal.—At the ends of shoots and terminating the season's growth.

Axillary.—Growing in the axils of leaves.

Lateral.—Growing from the side of the stem, usually in the axils of leaves.

Adventitious.—Growing from roots or leaves or in any unusual place, such as internodes.

Coverings:

Scaly.—Covered with scale-like leaves.

Hairy.—With the outer scales covered with hairs.

Resinous.—Exuding a sticky material.

Naked.—Without scale-like leaves covering the parts that are to become foliage leaves or floral parts.

LEAVES

Leaves are temporary organs having primarily the functions of transpiration, respiration, and photosynthesis, but often specialized for other purposes. They are always borne on the nodes of stems.

Duration:

Deciduous.—Falling off soon after maturity.

Persistent.—Remaining in place and functioning for 1 or more years after formation.

Evergreen.—Not deciduous. Persistent.

Fugacious.—Falling almost as soon as formed. Applied most often to stipules.

Arrangement on the Stem:

Alternate.—One leaf at a node and so arranged that a line drawn on the stem through the leaf bases will take a spiral course up the stem.

Opposite.—Two leaves at a node on opposite sides.

Whorled.—More than two leaves at a node in a circle around it.

Verticillate.—Same as whorled.

Trifoliate.—Having a whorl of three simple leaves.

Bract.—A relatively small leaf just below an inflorescence, flower, or floral part.

Subtend.—To enclose in its axil. Used in reference to a bract or a leaf to indicate its position below a bud, inflorescence, flower, or floral part.

Leaf Parts:

Blade.—The flat, expanded portion.

Petiole.—The leaf stalk (not to be called a stem).

Stipules.—Two scale-like attachments at the base of the petiole. They may be specialized into spines.

Sheath.—The basal portion of grass or sedge leaves surrounding the stem.

Ligule.—The extension at the top of the leaf sheath of grasses.

Dorsal Surface.—The application of this term to distinguish between the upper and lower surfaces of leaves is in a chaotic condition. Dorsal is from *dorsum* meaning back. In the animal kingdom the back is generally the upper surface. In the plant kingdom, however, it is conceived that the surface of the leaf away from the stem axis is the back, and as the leaf assumes a horizontal position this becomes the under surface. That the same term should be applied to the upper surface of an animal and of the thallus of a liverwort and to the lower surface of a leaf seems inconsistent, especially since it is but an analogy to call the surface of a leaf away from the axis the back. Hence there is a disposition among botanists to call the upper surface the dorsal and the lower surface the ventral, but usage is not uniform.

Ventral Surface.—The opposite of dorsal.

Absence of Parts:

Sessile.—Without petiole, the blade being attached directly to the stem.

Exstipulate.—Without stipules.

General Shape:

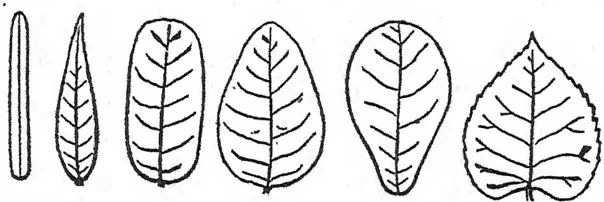
Linear.—Very narrow, with parallel margins.

Lanceolate.—Narrow, and tapering toward the ends like the head of a lance.

Oblong.—About twice as long as broad, with the sides nearly parallel through the middle portion.

Elliptic.—In the form of an ellipse.

Ovate.—Like the longitudinal section of a hen's egg, with the petiole attached to the broad end.



A B C D E F

FIG. 12.—Shapes of leaves. *A*, linear. *B*, lanceolate. *C*, oblong. *D*, ovate. *E*, obovate. *F*, cordate. (*After Gray.*)

Obovate.—Like ovate, but with the petiole at the narrow end.

Cordate.—Heart-shaped, especially with regard to the base.

Peltate.—With the petiole attached to the lower surface of the blade inside the margin.

Perfoliate.—The sessile blade clasping the stem, which appears to run through it.

Plicate.—With blade folded or plaited along the main veins.

Compounding:

Simple.—With the blade in one piece.

Compound.—With the blade divided into several distinct parts. Usually each of these parts (leaflets) is attached to the midrib or stalk by a definite articulation.

Trifoliolate.—Having three leaflets.

Unifoliolate.—With a single leaflet which is all that is left of a compound leaf, the other leaflets having been lost by reduction. Apparently simple. Examples, barberry and orange.

Leaflet.—One of the parts of a compound-leaf blade.

Rachis.—The extension of the petiole to which the leaflets of a pinnately compound leaf are attached.

Pinnate.—With the leaflets attached at different points along the rachis.

Palmate.—With the leaflets attached practically at the same point, at the end of the petiole.

Decompound.—With the leaflets compounded.

Margins:

Entire.—Without indentations of any sort.

Dentate.—With teeth pointing outward.

Denticulate.—Like dentate but with finer teeth.

Serrate.—With teeth pointing toward the apex.

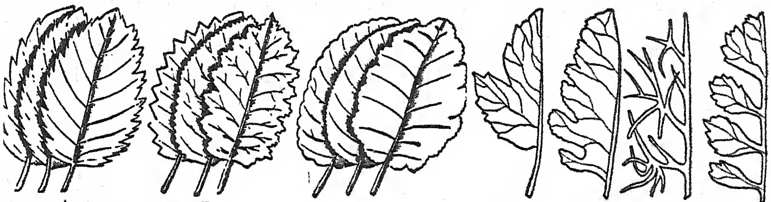


FIG. 13.—Margins of leaves. *A*, serrate. *B*, dentate. *C*, crenate. *D*, lobed. *E*, cleft. *F*, laciniate. *G*, divided. (*A, B, and C after Bastin.*)

Serrulate.—Like serrate, but with finer teeth.

Undulate.—With wavy surface at margin.

Lobed.—With relatively few large, shallow indentations.

Cleft.—With a few incisions extending halfway to the center or a little deeper.

Crenate.—With rounded or blunt teeth. Scalloped.

Divided.—With incisions extending to the midrib or main veins. Almost compound.

Laciniate.—With many deep, narrow incisions.

Base:

Cuneate.—The blade extending downward along the petiole.

Sagittate.—The base of the blade extended into two lobes that point downward or slightly inward.

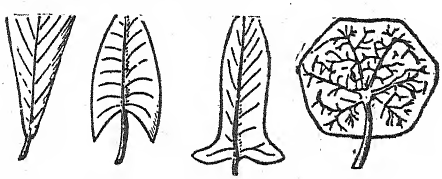


FIG. 14.—Bases of leaves. *A*, cuneate. *B*, sagittate. *C*, hastate. *D*, peltate. (*After Bastin.*)

Hastate.—Like sagittate, but with the basal lobes diverging from the petiole.

Apex:

Acuminate.—With a long, slender, sharp point, the margins near the tip being concave.

Acute.—With the point forming an acute angle, the margins near the tip being straight.

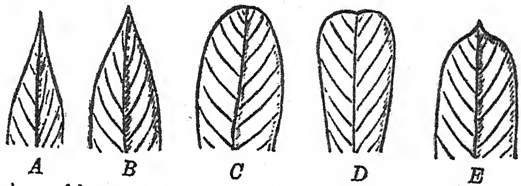


FIG. 15.—Apices of leaves. *A*, acuminate. *B*, acute. *C*, obtuse. *D*, emarginate. *E*, mucronate. (*After Bastin.*)

Obtuse.—Blunt-pointed.

Emarginate.—With a shallow notch at the tip.

Mucronate.—With a broad apex ending abruptly in a sharp tip.

Venation:

Veins.—Vascular bundles of leaves.

Midrib.—A large main vein running lengthwise through the blade from petiole to tip.

Parallel.—Running side by side without branching or intersecting.

Netted.—Running in all directions, branching and intersecting.

Reticulate.—Same as netted.

Palmate.—The main veins radiating from the point where the petiole joins the blade.

Pinnate.—Having a midrib with smaller veins branching from it.

Surface Coverings:

Glabrous.—Without hairs of any kind.

Glaucous.—Covered with a whitish waxy coating (bloom) that easily rubs off.

Pubescent.—With fine, soft, short hairs.

Villous.—With long, silky, straight hairs.

Hirsute.—With moderately stiff hairs.

Hispid.—With stiff, bristly hairs.

Tomentose.—With long, curled, matted hairs (woolly).

Texture:

Succulent.—Having much parenchyma and little mechanical tissue.

Chartaceous.—Having parchment-like texture.
Scarious.—Thin and dry, but neither green nor transparent.
Hyaline.—Transparent or translucent.
Coriaceous.—Rather thick and tough. Leathery.

INFLORESCENCES

When flowers are borne close together, thus forming a natural cluster, this is called an inflorescence. An inflorescence is, in reality, a closely branching stem, each branch bearing a flower. If the branches are far apart, the term "inflorescence" is not applied, and naturally this is an intergrading character. Some inflorescences are clear-cut, typical, and easily distinguished. Others may grade into each other or be so irregular that they are hard to recognize by description.

Compounding:

Simple Inflorescence.—One in which only the main flower stem branches.

Compound Inflorescence.—One in which the flower stems branch two or more times.

Parts:

Rachis.—The central axis of an inflorescence.

Pedicel.—The individual stalk of each flower in an inflorescence.

Peduncle.—The stalk bearing an inflorescence or a solitary flower.

Types:

Indeterminate.—With flowers opening in succession rather than simultaneously. The lower or outside ones open first and in extreme cases new buds continue to appear at the tip throughout the season.

Determinate.—With the first flower bud forming at the tip of the axis or rachis of the inflorescence and thus stopping its terminal growth, the other flowers on the branches below opening a little later.

Raceme.—An indeterminate inflorescence consisting of a central rachis bearing pediceled flowers along its sides, the different pedicels about equal in length when mature.

Spike.—An indeterminate inflorescence consisting of a central rachis bearing sessile flowers along its sides. Spikes and racemes are intergrading.

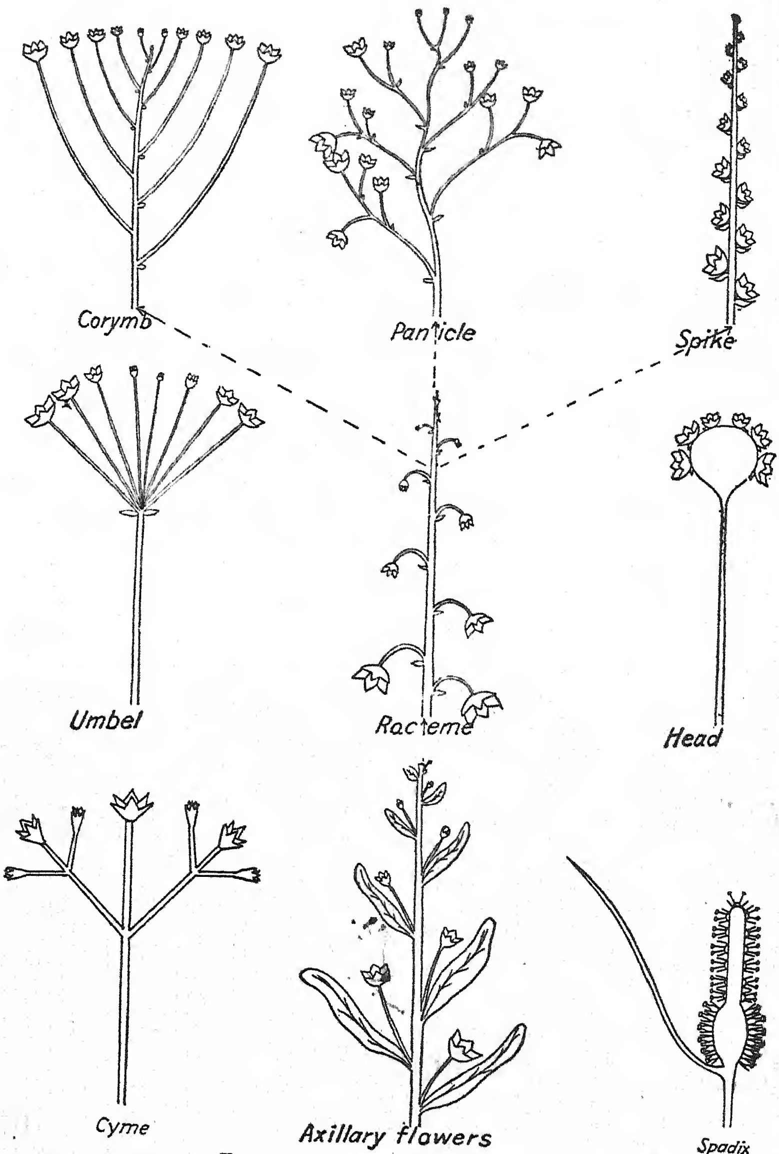


FIG. 16.—Types of inflorescences.

Ament.—A spike bearing apetalous unisexual flowers. It is usually pendulous and deciduous.

Catkin.—Same as ament.

Corymb.—An indeterminate inflorescence consisting of a central rachis with pediceled flowers along its sides, the lower pedicels much longer than the upper, giving the inflorescence a flat or rounded top. The outside flowers borne by the lower pedicels open a little earlier than the central upper ones. Corymbs and racemes are intergrading. Simple corymbs are rather rare.

Head.—A compact indeterminate inflorescence, with sessile flowers attached as nearly as possible at one point, *i.e.*, on the expanded top of the stem. Heads intergrade with spikes, racemes, and umbels.

Umbel.—An indeterminate inflorescence with several pediceled flowers attached practically at the same point on the top of the stem. The outside flowers open in advance of the inner ones. In general effect the umbel and corymb are similar in appearance, the difference being in the attachment of the pedicels.

Panicle.—An indefinitely branching inflorescence. It is practically a long-pediceled, loosely branching, compound raceme or corymb.

Cyme.—A few-flowered, flat-topped, determinate inflorescence in which the central terminal flowers open slightly in advance of the outer ones. Most cymes occur on plants with opposite leaves or in axillary clusters.

Scorpioid Cyme.—One in which the central axis is coiled, especially before the flower buds open, with the flowers on the convex side of the rachis.

Spadix.—An inflorescence consisting of a fleshy central column bearing many stamens below and many pistils above. The spadix is surrounded by a large bract or spathe, usually showy, giving the whole the effect of a single flower.

FLOWERS

Flowers are the special reproductive systems of the Spermatophyta. Some would restrict the term "flower" to the angisperms, thus excluding the strobilus of the gymnosperms. A functional flower must contain at least one microsporophyll (stamen) or macrosporophyll (carpel). Most flowers contain

several of each and certain accessory organs, *i.e.*, petals and sepals.

The normal arrangement of floral organs is in four whorls or circles in the following order from the outside inward: (1) sepals (calyx), (2) petals (corolla), (3) stamens (androecium), and (4) pistils (gynoecium).

Floral Organs.—Certain parts of the flower are specialized stems, *viz.*:

Receptacle.—The expansion at the top of the peduncle that bears the carpels and other floral organs.

Torus.—Same as receptacle.

Hypanthium.—The cup-shaped receptacle of a cotyloid flower.

The other floral organs are specialized leaves. They are

Calyx.—The collection of sepals that encloses the rest of the organs in the bud.

Corolla.—The circle of petals just inside the calyx and usually forming the showy part of the flower.

Ligule.—(1) In Compositae, the strap-shaped extension of the corolla of the ray flowers. (2) In Gramineae, the collar-like extension of the leaf sheath clasping the stem above the attachment of the blade.

Stamen.—A microsporophyll found just inside the corolla and producing the pollen grains.

Filament.—The microsporangiophore or stalk of the stamen.

Anther.—The microsporangium, which contains the pollen grains (microspores).

Staminode.—An abortive stamen, usually the filament only, which may even be reduced to a scale or tiny projection.

Pistil.—The central organ of the flower, composed of one or more carpels that may be united completely or only at the base.

Carpel.—A macrosporophyll enclosing one or more ovules (macrosporangia).

Ovule.—The body that develops into a seed.

Ovary.—The expanded basal portion of the pistil, containing the ovules.

Stigma.—The tip of the pistil, which is receptive to the pollen grains and on which they germinate.

Style.—The slender portion that connects the ovary with the

stigma and holds the latter in position to receive the pollen grains.

Bract.—A leaf or scale in whose axil an inflorescence, flower, or floral organ is produced.

Spathe.—A large, usually showy, bract at the base of a spadix or other inflorescence and enclosing it.

Involucre.—A series of scale-like leaves at the base of a flower or an inflorescence.

Sexuality:

Complete.—Containing all the different kinds of floral organs.

Bisexual.—With both stamens and pistils.

Perfect.—Same as bisexual.

Hermaphrodite.—Same as bisexual.

Unisexual.—With stamens or pistils but not both.

Imperfect.—Same as unisexual.

Staminate.—With stamens but not pistils. Also called male.

Pistillate.—With pistils but not stamens. Also called female.

Monoecious.—Each individual plant producing both staminate and pistillate flowers.

Dioecious.—Each individual plant bearing staminate or pistillate flowers but not both.

Polygamous.—The same or different individual plants producing both bisexual and unisexual flowers.

Anemophilous.—Adapted for wind pollination.

Entomophilous.—Adapted for insect pollination.

Floral Axis:

Strobiloid.—With a convex or flat receptacle to which the other floral organs are united.

Cotyloid.—With a receptacle that is concave, sometimes to the extent of surrounding the carpels.

Insertion:

Hypogynous.—Calyx, petals, and stamens attached to the receptacle at the base of the ovary, which is superior. Applies to strobiloid flowers.

Perigynous.—Petals and stamens attached to the margin of a cup-shaped extension of the receptacle (hypanthium) or united to the calyx tube and apparently growing from it. At least the upper half and usually all of the ovary is free from the surrounding parts. Applies to cotyloid flowers.

Epigynous.—Sepals, petals, and stamens apparently growing from the top of the ovary but in reality from the hypanthium, which extends up around the ovary and adheres to it. Applies to cotyloid flowers.

Arrangement of Floral Parts:

Aestivation.—The arrangement of floral parts in the bud. Some restrict the term to the perianth.

Imbricated.—With the sepals or petals overlapping each other at the margins.

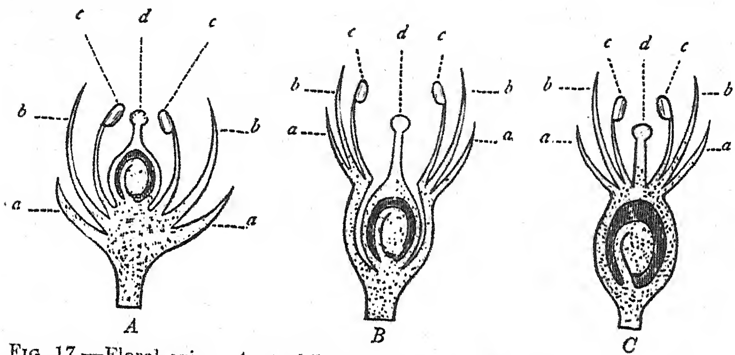


FIG. 17.—Floral axis. *A*, strobiloid flower, showing hypogynous insertion of sepals, petals, and stamens. *B*, cotyloid flower showing perigynous insertion, the receptacle extending to form an hypanthium. *C*, epigynous insertion in cotyloid flower. (*After Bastin.*)

Valvate.—With the sepals or petals abutting at their margins but not overlapping.

Number of Floral Parts:

-merous.—An ending which, taken with a numerical prefix, indicates the number of each of the floral parts. For example, in a 5-merous (pentamerous) flower, sepals, petals, sometimes stamens, and carpels are in fives or multiples of five.

Union of Parts:

Symphysis.—The union of like parts with each other in the process of formation, as the symphysis of petals.

Coalescence.—Same as symphysis.

Cohesion.—Same as symphysis.

Connate.—United with like members in the process of formation, as filaments connate with each other.

Adnate.—United with a different kind of organ in the process of development, as the calyx tube adnate to the ovary.

Adherent.—Same as adnate.

Free.—Not adnate, as the ovary free from the receptacle.

Distinct.—Not connate or coalescent, as the sepals distinct from each other.

Connivent.—Coming together without uniting, or but slightly adherent.

Calyx:

Distinct.—Sepals not united to each other.

Tubular.—Sepals united to each other except at the toothed margins.

Nerve.—Vein in a sepal, petal, carpel, bract, or scale.

Pappus.—Bristles or scales on an achene, representing the persistent calyx.

Perianth.—Calyx and corolla collectively.

Scabrous.—Rough and harsh to the touch.

Scarious.—Thin and dry, with little or no chlorophyll.

Corolla:

Apetalous.—Without petals, or the petals reduced to inconspicuous scales.

Polypetalous.—Each petal distinct from the others.

Gamopetalous.—With petals united to each other at their margins to form a tube or funnel.

Monopetalous.—Same as gamopetalous.

Sympetalous.—Same as gamopetalous.

Regular.—With all petals of the same shape.

Actinomorphic.—Same as regular.

Symmetrical, or Radially Symmetrical.—Same as regular.

Irregular.—Bilaterally symmetrical, with petals of different shapes.

Zygomorphic.—Same as irregular.

Stamens:

Androecium.—The collection of stamens in a flower.

Monadelphous.—With filaments united into a tube or column.

Diadelphous.—With filaments united into two sets.

Versatile.—The anther attached near the middle to the tip of the filament.

Introrse.—The anther facing the center of the flower.

Extrorse.—The anther facing the periphery of the flower.

Staminode.—A sterile stamen, *i.e.*, one that has no functional anther and may be reduced to only a tiny projection representing the base of a filament.

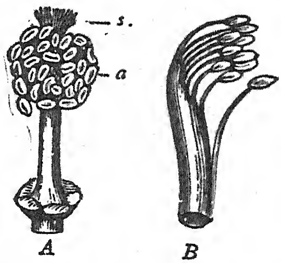


FIG 18.—Coalescence of stamens. *A*, monadelphous. *B*, diadelphous. (*After Bastin.*)

Pistils:

Gynoecium.—The collection of carpels in a flower, whether separate or united into one pistil.

Inferior Ovary.—Embedded in the receptacle, resulting in an epigynous insertion of petals and stamens.

Superior Ovary.—Set on top of the receptacle, with the insertion of petals and stamens hypogynous or perigynous.

Simple.—A unicarpellate pistil.

Compound.—A pistil of two or more united carpels. It may contain one or more chambers.

Cell.—One of the chambers or cavities in a pistil, containing the ovules. A rather unfortunate term owing to its different meanings.

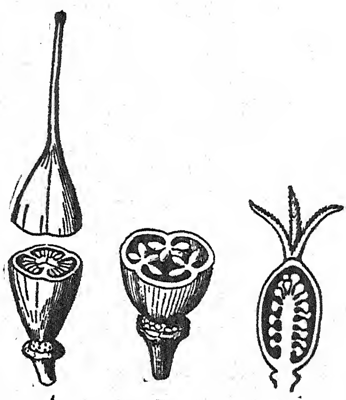


FIG. 19.—Placentation. *A*, axile. *B*, parietal. *C*, free central. (*After Gray.*)

Placenta.—The part of the ovary to which the ovules are attached. This is usually the margin of the carpel.

Axile Placentation.—Each carpel entirely closed, thus making as many chambers as carpels, with the placentae at the center of the pistil (if compound).

Parietal Placentation.—Each carpel more or less open, with margins of adjacent ones coherent, thus forming a one-chambered compound ovary with placentae on the walls at the lines of union.

Central Placentation.—In an ovary of more than one carpel, the ovules attached to a compound placenta that rises as a column from the base. This column may be formed by the suppression of the portion of the carpels that forms the partition or by an extension of the carpels where they join at the base.

Ovules:

Orthotropous.—The ovule symmetrical and straight with the chalaza at the base and the micropyle at the tip.

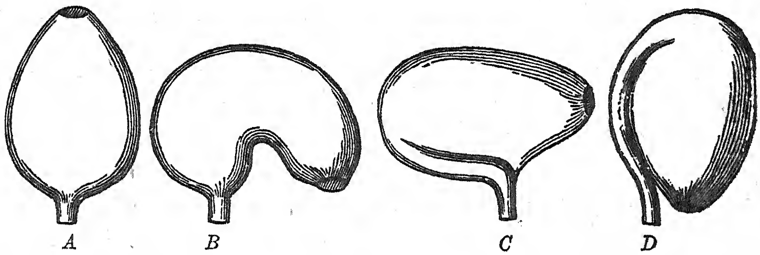


Fig. 20.—Types of ovules. *A*, orthotropous. *B*, campylotropous. *C*, amphitropous. *D*, anatropous. (*After Bastin.*)

Anatropous.—The ovule symmetrical but completely inverted so that the apparent tip is really the chalaza and the micropyle is close to the stalk, which is adnate the entire length of the ovule.

Amphitropous.—The ovule symmetrical but half inverted, so that the stalk appears to be attached at the side.

Campylotropous.—The ovule asymmetrical and curved so as to bring the base and micropyle close together.

FRUITS

Strictly speaking, the true fruit is a ripened ovary It may, however, have various appendages—receptacle, involucre, calyx, style, etc.—which are commonly included under the term "fruit."

Parts of Wall.—Many fruits have three layers in the wall, but these may be intimately blended.

Pericarp.—The wall of the fruit considered as a whole.

Exocarp.—The outer layer of the pericarp, including the skin.

Mesocarp.—The middle layer of the pericarp.

Endocarp.—The inner layer of the pericarp, including the lining wall of the seed chamber.

Character of Wall:

Fleshy.—Relatively soft and juicy.

Dry.—Relatively hard and tough.

Dehiscent.—Opening naturally, in the case of a dry fruit, to permit the escape of the seeds.

Suture.—The line along which the parts separate in dehiscence.

Valve.—One of the segments into which the walls of a fruit separate by dehiscence.

Kinds of Fruit:

Simple.—Composed of a single ripened ovary.

Aggregate.—Composed of several ripened ovaries from a single flower, joined together by a common receptacle.

Multiple.—The ripened ovaries of several flowers borne in a compact spike and joined together in maturity.

Pod.—A unicarpellate fruit, generally dehiscing along both dorsal and ventral sutures.

Legume.—Same as pod (also the common name of any member of the Leguminosae).

Follicle.—A unicarpellate, dry fruit, with one to several seeds, dehiscing along the ventral suture.

Loment.—A segmented pod.

Capsule.—A many-seeded, dry, usually dehiscent fruit. Generally applied to those of two or more carpels.

Silique.—A special long, slender capsule of two carpels, found in the mustard family.

Silicle.—A special short, broad capsule of two carpels, found in the mustard family.

Achene.—A small, dry, indehiscent, one-seeded fruit, the seed readily separating from the ovary wall. It may be either plumed or naked.

Caryopsis.—A seed-like fruit resembling an achene but having the seed coat firmly united to the ovary wall. Especially common in the Gramineae.

Samara.—Like an achene but winged.

Utricle.—An achene with a loose involucral covering.

Nut.—Like an achene but larger, and usually resulting from a compound ovary. It is generally enclosed in a husk composed of a developed involucre.

Pome.—A several-carpellate, several-seeded, fleshy fruit, in which the wall is a combination of carpels and receptacle. It results from the development of an inferior ovary with its appendages.

Drupe.—A one-seeded, fleshy fruit, developed from a superior ovary, the endocarp taking the form of a hard "stone." The term is sometimes restricted to unicarpellate fruits.

Berry.—A several-carpellate, several-seeded, fleshy fruit with pericarp entirely soft. It may be formed from either an inferior or a superior ovary. It differs from a pome in having the carpels soft in texture.

SEEDS

The seed is a ripened ovule. It consists of the wall of the macrosporangium, the nucellus (which may be more or less absorbed), one or more seed coats, and an embryonic plant. Many seeds contain also an endosperm, developed from the female gametophyte and richly stored with food.

Parts of the Seed:

Integument.—One of the layers (of which there are usually two) that grow around the macrosporangium from its base and form the walls of the ovule and hence the seed coat.

Testa.—The outer covering of a seed. The seed coat.

Endosperm.—The tissue that stores food outside the embryo. It originates from a union of the second sperm nucleus with the primary endosperm cell.

Embryo.—The young plant developed from the fertilized egg cell.

Funiculus.—The stalk of an ovule or a seed.

Hilum.—The scar on a seed left by its separation from the funiculus.

Chalaza.—The place where the seed coats unite with the rest of the ovule.

Micropyle.—An opening where the integuments have not completely grown over the ovule. The pollen tube grows through this opening to fertilize the egg cell.

CHAPTER V

GENERAL FEATURES OF SPERMATOPHYTA

The Spermatophyta or seed-bearing plants have formed the most conspicuous part of the vegetation of the earth for millions of years, since the middle of the Paleozoic era (see frontispiece). From the time of their origin their superiority over other plants in fitness to inhabit the land asserted itself, and their increase in numbers, size, and diversity of form was rapid.

It is well to keep in mind that the seed-bearing habit appears to have originated several different times at widely separated intervals, some of the lines now being extinct. While botanists have long divided the Spermatophtya into two classes (or subclasses), Gymnospermae and Angiospermae, there is considerable doubt that either one is monophyletic. It is quite likely that those living today, and generally included under the name Spermatophyta, are polyphyletic. Concerning the Angiospermae, Campbell gives the following opinion:

"Notwithstanding the unmistakable relationships existing among the Angiosperms, it is becoming more and more evident that their arbitrary division into two co-ordinate subclasses, Monocotyledons and Dicotyledons, is not entirely natural. That there have been more than two main lines of evolution from some older stock that no longer exists seems certain; and it is much more likely that instead of two primary divisions or subclasses we should recognize a much greater number—subclasses or phyla based upon something more than the superficial characters which often are deemed sufficient."[1]

The best known of the Spermatophyta are the conifers and flowering plants. There are some differences in the use of the term "flower." Some would restrict it to the usually showy reproductive and accessory organs found in the angiosperms, while others would include under it the strobili of the gymno-

[1] CAMPBELL, D. H., "The Evolution of the Land Plants," p. 563, Stanford University Press, 1940.

sperms. Likewise, there is an erroneous tendency to use the term "conifer" as synonymous with "gymnosperm," whereas it should be restricted to the one order Coniferales.

Most of the seed plants are autophytic, *i.e.*, possessed of chlorophyll and therefore not dependent on organized material for nutrition. A few, however, are saprophytic or parasitic to a greater or less degree. The great majority are terrestrial, but a few have adopted an epiphytic habit, while here and there throughout the group members have invaded shallow waters and become adapted to an aquatic life.

The Spermatophyta form by far the largest of the four divisions of the plant kingdom, including nearly 200,000 species. These are grouped into some 300 families, of which approximately two-thirds are represented in the United States. The number of families cannot be stated exactly, for authorities differ as to what constitutes a family in certain cases. In some systems of classification such families as Liliaceae, Rosaceae, Leguminosae, and Compositae, which contain large numbers of genera, are preserved, while in other systems each of these is broken up into two or more smaller families.

The Spermatophyta also show the greatest variation in size of any of the four divisions of plants. They include all of the giant trees, some of which are 30 feet or more in diameter, and range down to tiny flowering plants a fraction of an inch high—smaller than the average pteridophytes and bryophytes and much smaller than many of the algae and fungi. Some are called mosses by those unfamiliar with plant classification.

In no other division is there growth by a cambium layer separating phloem and xylem, a character found in gymnosperms and most dicotyledons.

CLASSIFICATION OF SEED PLANTS

To show the relationships recognized in the larger subdivisions of the seed plants, the following synopsis of classification is submitted.

DIVISION SPERMATOPHYTA

Plants with true roots, stems, and leaves that belong to the sporophyte generation, the gametophytes being reduced to very small size. Reproduction is by seeds, sometimes supplemented by vegetative propagation.

Class I. GYMNOSPERMAE

Strobili unisexual or bisexual, the female producing naked ovules, *i.e.*, ovules and resulting seeds not enclosed in carpels. Vascular bundles collateral and arranged in a cylinder about a pith. The xylem region contains tracheids but no tracheae in the secondary xylem (excepting in the Gnetales) (see page 89). The female gametophyte (except in Gnetales) is multicellular and contains several archegonia. The male gametophyte is very much reduced. In the orders Cycadales and Ginkgoales it produces motile gametes, indicating an aquatic ancestry, but in the higher Coniferales nonmotile germ tubes have replaced them.

Class II. ANGIOSPERMAE

Plants with true flowers, each containing, normally, four whorls of floral organs. The ovules are enclosed in carpels that may be distinct or united into a compound pistil. The vascular bundles are collateral and either arranged in a cylinder surrounding a pith or scattered through the pith. The xylem region contains fibers and tracheae. The female gametophyte produces no archegonia and is reduced to eight cells (or to one cell with eight nuclei). The male gametophyte is the germinated pollen grain, with nonmotile cells—usually three.

Subclass 1. Dicotyledones.—Floral parts usually in multiples of five or four. Two cotyledons in each seed (rarely one). Vascular bundles usually in a cylinder with a cambium layer separating phloem and xylem. Leaves with netted veins.

Subclass 2. Monocotyledones.—Floral parts usually in multiples of three. One cotyledon in each seed, often with the rudiment of another. Vascular bundles usually scattered through the pith and without cambium. Leaves with parallel veins (rarely netted).

CHAPTER VI

FAMILIES OF GYMNOSPERMS

The gymnosperms consist mostly of shrubs and trees, some of gigantic size. They were once the predominant vegetation of the earth but have long been gradually declining in numbers (see frontispiece). They are of ancient lineage, perhaps from as far back as Cambrian times, some 400 million years ago, but reached the climax of their abundance in the Pennsylvanian (Upper Carboniferous) period about 250 million years ago. Since that time they have gradually become fewer, many species now being entirely extinct. While other orders waned, the Coniferales greatly increased in number and size of individuals, and this has become the predominant order of the class.

General Appearance.—In the general appearance of the vegetative portion some gymnosperms resemble large, coarse ferns, some are suggestive of certain kinds of palms, while most of those in the North Temperate Zone are forest trees—the pines, spruces, firs, etc., with which most of us are familiar. The great majority are evergreen, *Larix* spp. being an exception.

Gymnosperms are the most ancient of the seed plants. There is no doubt that they evolved from pteridophytes, probably heterosporous ferns, and the seven orders (three of them extinct) fall naturally into two groups or subclasses as indicated by Chamberlain.[1] These two lines may have originated separately or as one that soon branched. Fossil evidence leaves the question unsettled.

Classification.—The following classification is used by Chamberlain in the work already cited:

Cycadophytes
- Order Cycadofilicales (extinct)
- Order Bennettitales (extinct)
- Order Cycadales

[1] CHAMBERLAIN, CHARLES J., "Gymnosperms," Stanford University Press, 1935.

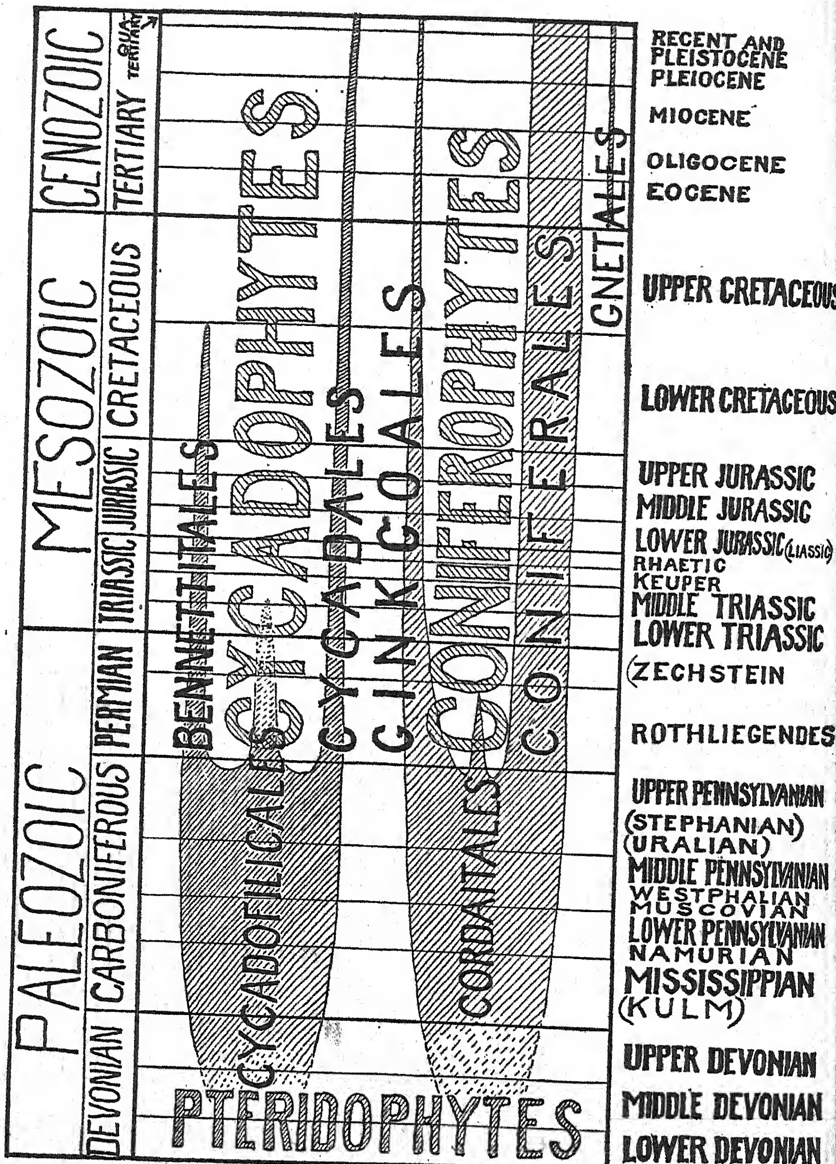


FIG. 21.—A conjectural position of the various gymnosperm groups in geological time. The horizons were compiled by Dr. A. C. Noé from various sources. The comparative amount of space does not equal the comparative amount of time. (*From C. J. Chamberlain.*)

Coniferophytes
- Order Cordaitales (extinct)
- Order Ginkgoales (nearly extinct)
- Order Coniferales
- Order Gnetales (nearly extinct)

A comparison of the size and general appearance of the Cycadophytes and the Coniferophytes is shown in Fig. 22. In general, the former is characterized by an unbranched trunk with large compound leaves and the latter by a branching trunk with small, narrow, simple leaves.

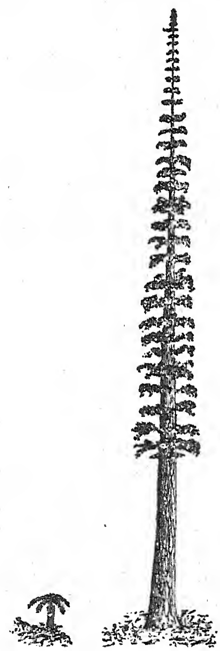


FIG. 22.—The habit and comparative size of members of the Cycadophytes and Coniferophytes. (*From C. J. Chamberlain.*)

ORDER I. CYCADOFILICALES

This extinct order is probably the oldest of the gymnosperms. Fossil remains are found in Devonian strata, and the origin of the group may have been still earlier. The climax of abundance and specialization occurred in the Carboniferous period, after which the decline was rapid. Many of the fern-like fossils commonly found in coal are Cycadofilicales, as shown by their production of seed, which caused the English botanists to call them "seed ferns" (Pteridospermae).

Vegetative Structures.—The most primitive of the group lacked the broad fronds characteristic of the ferns of today, having only small, narrow, branching leaf stalks, in which respect they were much like the primitive true ferns of the same period. This suggests either that this ancient order of gymnosperms came from primitive ferns or that the two had a common ancestry and followed a parallel course in leaf development until, in the Carboniferous period, broad fronds were the rule in both.

The fibrovascular system varied greatly with the species. In some it was like that of our common ferns; in others the stem had

a cortex surrounding a stele of phloem and xylem with a cambium layer between and a pith in the center.

Reproduction.—In reproduction two kinds of spores were formed on the fronds or in place of them. Some of these were produced in sporangia much like those of ferns and functioned as pollen grains that seem, in some cases at least, to have developed motile antherozoids. Others were formed within scaly coverings and produced ovules that, when fertilized, became seeds. These seeds became dormant shortly following fertilization, before an embryo was produced.

Order II. BENNETTITALES

This order probably branched from the Cycadofilicales in the Carboniferous period, although no fossils have been found earlier than the Permian. The maximum development occurred in the Jurassic. Their end seems to have come in the Cretaceous period, and all forms are now extinct. Probably this order ran the shortest course, geologically, of any of the gymnosperms. They were abundantly distributed throughout the United States and Mexico, and some specimens have been found in Europe.

Vegetative Characters.—The commonest form of the Bennettitales was a stocky, unbranched trunk 2 or 3 feet high, surmounted by a crown of large, pinnately compound leaves. However, some of the trunks were scarcely taller than broad, and in one genus the stem was rather slender and branched.

Reproduction.—The most characteristic structures of the Bennettitales were the strobili. They were very numerous in the axils of the leaves and were bisexual. A typical strobilus had the superficial appearance of a flower. Above a rosette of leaves there formed numerous compound sporophylls bearing sporangia filled with pollen grains. These surrounded a central cone bearing numerous short-stalked ovules, each having a characteristic micropyle. The presence of pollen tubes or antherozoids has not been established. Within the seed a dicotyledonous embryo was formed.

The flower-like structure of the bisexual strobilus and the dicotyledonous seed have led some taxonomists to believe that the Bennettitales were the direct ancestors of angiosperms of the *Magnolia* type, but this idea is strenuously opposed by Chamberlain.[1]

[1] *Loc. cit.*, p. 59.

ORDER III. CYCADALES

From the fossil remains we find evidence that the Cycadales first appeared in the late Carboniferous period, became more abundant during the early Mesozoic era, and then declined, leaving at the present time only one family with nine genera and less than a hundred species. They were formerly widely distributed and abundant. The living forms are mostly tropical and subtropical, being especially abundant in Mexico and the West Indies, South Africa, and Australia. In a few places they form a conspicuous part of the dense vegetation, but generally they are scattered. It is believed that their ancestors were Cycadofilicales.

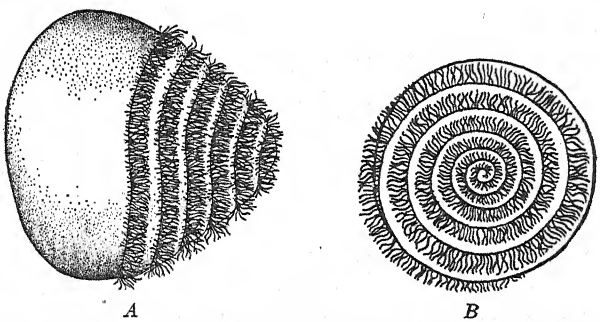


FIG. 23.—Spermatozoids of *Zamia floridana*. *A*, side view, showing spiral band of cilia. *B*, apical view. (*Redrawn after Webber.*)

Vegetative Structures.—The vegetative structure of the living Cycadales is fern-like, with large, pinnately compound fronds and usually short, stout stems, although the stems of some fossil forms were very slender. They are seldom more than a few feet high.

Reproduction.—Among the fossil Cycadales the spores of some species were borne on the fronds, and in others they were in strobili. In present-day Cycadales all species are dioecious. The female strobili of some species are of huge size, 3 feet or longer. The pollen grains germinate and form tubes that require several months to penetrate the nucellus, from which they absorb food and thus function as haustoria. In the basal portion of the pollen tube are produced motile antherozoids that are of unusual size and complexity. Some are actually visible to the unaided eye and bear hundreds of cilia. Following fertilization an embryo is formed that becomes dormant as the seed ripens—an advance over the Cycadofilicales.

Order IV. CORDAITALES

Of the four orders of the coniferophytes, the Cordaitales is the only one that is extinct, although two others are nearly so. Like the Cycadofilicales, the Cordaitales appeared in the Devonian period or earlier, but whether the latter evolved from primitive members of the former, making the gymnosperms monophyletic, or whether the two evolved separately, making the class diphyletic, is still uncertain. The Cordaitales reached their maximum profusion in the Carboniferous period, when they were world-wide in distribution, but seem to have disappeared in the Permian, making them the first of the gymnosperms to become extinct.

Vegetative Characters.—In their prime the Cordaitales formed great forests, some of the trees being 100 feet high with trunks up to 3 feet in diameter. The leaves were simple and in some species very large, as much as 3 feet in length, but more commonly only a few inches. Usually the trunks were bare for a considerable distance, the upper half being much branched.

Reproduction.—The micro- and macrosporangia were borne in separate strobili; some species were monoecious while others were dioecious. Both kinds of strobili were borne on stalks, the male sporangia being more numerous than the ovules. Antherozoids have not been found, but it is believed that they existed. Study of the fossilized seeds has been rather meager, and embryos have not been found in them.

Order V. GINKGOALES

This order was never so abundant as those just described, either in number of species or wealth of individuals. It appears to have originated from the Cordaitales in the Carboniferous period and to have reached its greatest abundance in the Permian. At the present time only one living species remains, *Ginkgo biloba*, the maidenhair tree of China and Japan. It is not even certain that this tree is still found growing wild, although a few specimens have been reported in western China by travelers. Some authorities believe that this tree would have become extinct but for its culture as an ornamental tree.

It is an interesting fact that this species has undergone no detectable change for more than 150 million years, nor is it known to have given origin to any other species, although some of the

fossils may represent other species of the same genus. *Ginkgo biloba* has been very thoroughly studied and will be used as the basis for further description of this order.

Vegetative Structures.—*Ginkgo biloba* is a large, beautiful tree, grown extensively in the Orient and introduced into many parts of the United States and Europe where the climate is not too severe. The leaves are deciduous and very characteristic in appearance. They are broad, rather thick, glossy, and fan-shaped, with conspicuous, dichotomously branched veins radiating from the end of the petiole to the margin. Many of the leaf petioles are branched into two lobes. The wood shows definite annual rings and a small pith.

Reproduction.—The trees are dioecious. The male and female strobili, on separate trees, are borne on short stalks. The male strobilus is compact and consists of a large number of sporophylls, each bearing, as a rule, two microsporangia. The female strobilus is a loosely branching structure bearing a few ovules, which are generally in pairs.

The pollen grains form germ tubes, which, like those of the cycads, function as haustoria in the nucellus, and two large antherozoids are produced in the base of each.

In each of the ovules there forms an oval, many-celled gametophyte containing two archegonia. After fertilization, a dicotyledonous embryo develops, and as the seed ripens, its outer portion becomes soft and fleshy like a fruit. It has a disagreeable odor, and for this reason staminate trees are sometimes preferred to pistillate for ornamental planting.

ORDER VI. CONIFERALES

The best known of the gymnosperms are the Coniferales, which form almost the exclusive forest type in many cold, semiarid regions and are widely distributed, especially in the North Temperate Zone and extending to the arctics.

The Coniferales[1] appear to have come from the Cordaitales in the Permian period and to have reached their climax in number of genera and species in the Cretaceous, but they are still very abundant—perhaps more in number of individuals now than in prehistoric times.

[1] The common name "conifer" should not be used as a synonym of "gymnosperm" but restricted to the order Coniferales.

Vegetative Characters.—A few of the Coniferales are low shrubs, but most of them are trees, some of gigantic size, and usually they are evergreen. The stem structure is essentially like that of the dicotyledons, but the wood lacks the tracheae of angiosperms.

Reproduction.—There is considerable variation in the strobili of the Coniferales. Some are dioecious but more are monoecious, and a few have bisexual strobili. The pollen grains produce pollen tubes but no antherozoids. The ovules produce archegonia in which embryos are developed following fertilization.

Since this order of gymnosperms is now more important than all the others combined, it will be described in greater detail.

1. PINACEAE. Pine Family

A very important family of cone-bearing, mostly evergreen trees, containing about 8 genera and 150 species. They are of world-wide distribution, extending even to lofty mountain sides and far into northern regions. The Pinaceae were more abundant during the later Cenozoic era (see page 78) than now, but they have held their own better than most of the gymnosperms, probably because of their greater adaptability to the cold, dry climates that in most parts of the temperate zones replaced the subtropical conditions which prevailed before the Glacial epoch. The Pinaceae and other conifers may be looked upon as the highest evolutionary development of the gymnosperms. Even so, they doubtless are not the direct ancestors of the angiosperms but rather a somewhat specialized side branch of the main genetic line.

Familiar Examples.—The best known examples of the pine family are pine (*Pinus* spp.), Douglasfir (*Pseudotsuga* spp.), hemlock (*Tsuga* spp.), fir (*Abies* spp.), spruce (*Picea* spp.), and larch or tamarack (*Larix* spp.).

Stems and Roots.—The Pinaceae are all woody and are, for the most part, stately trees with straight, slightly tapering trunks, sometimes more than 250 feet high and 10 feet in diameter. The root system is generally wide-spread but not deep. The wood of the Pinaceae, like that of most gymnosperms (except Gnetales), differs from that of angiosperms in lacking tracheal vessels in the secondary xylem, their place being taken by tracheids. All parts

of the tree contain intercellular resin ducts, which become nonfunctional in the old heartwood.

Leaves.—The Pinaceae all have rather thick, linear, alternate leaves. In the pines they are 1½ to 12 inches long, but in the other genera they are shorter. This reduced leaf surface combined with a sunken condition of the stomata results in low transpiration, and the trees are thus able to survive in dry or frozen soils. With the exception of the larches or tamaracks the Pinaceae are evergreens, *i.e.*, they are clothed with foliage the year round. Each leaf persists on the tree from 3 to 10 years, depending on the species, but ultimately falls off. In addition to the regular foliage leaves the pines have scales, sometimes called primary leaves, on the buds and young shoots. These are relatively broad and thin, and deciduous. In the pines the leaf bases are enclosed in sheaths—one, two, three, four, or five leaves (depending on the species) growing from each sheath. In the other genera the leaves are single. The evergreen species have leaves of a very dark green, giving a somber appearance to the forests that they compose.

Strobili.—All members of this family are heterosporous, producing microspores in male strobili and macrospores in female strobili, both borne on the same tree. In the male strobili pollen sacs are borne on the underside of each scale, and in the female strobili two ovules are borne on top of each scale.

Seeds.—The seeds mature in ½ to 3½ years after fertilization. They are produced in large woody cones that open to release them. In most species each seed bears a broad wing that causes it to spin around in falling and so delays its descent that even a light wind will carry it to a considerable distance. The seed contains a relatively large endosperm and a straight embryo, usually with several cotyledons.

Economic Significance.—The Pinaceae are of great importance to mankind. But for this family of trees our familiar frame buildings could hardly exist. Pine, fir, spruce, and hemlock are not only more abundant than other kinds of lumber, but they are easy to work and do not warp badly when exposed to the weather. The turpentine that is an essential ingredient of ordinary paint and the rosin of varnish are extracted chiefly from pine stumps. The wood of this family is not of the highest grade for fuel, but because of its abundance in many regions where the hardwoods

are lacking it is a great asset and is extensively used. Enormous quantities are utilized for making certain grades of paper. Lastly, the forests of pine and other conifers cover many dry, rugged mountain sides that would be desolate without them and thus conserve the moisture and beautify the landscape. Where mixed with the light-green, broad-leaved forest trees the darker colors of this family give a most pleasing effect.

2. TAXODIACEAE. Taxodium Family

This family, once one of the most conspicuous on earth, is now reduced to eight genera, nearly extinct in the United States and

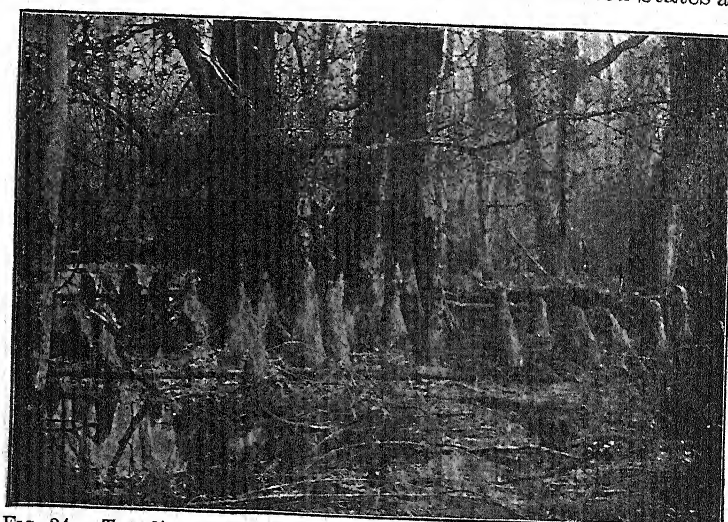


FIG. 24.—*Taxodium* (Taxodiaceae) showing natural habitat in swamp. The "knees" are formed by angles of the roots projecting above the mud and water. (*After Bergen and Caldwell.*)

widely scattered over the rest of the world. They are adapted to warm, moist climates, and throughout most of the Cenozoic era, especially the Miocene epoch, in the balmy climate that generally prevailed, their gigantic forms covered almost the entire Northern Hemisphere with a few extensions into the Southern.

Familiar Examples.—The Taxodiaceae are rare in the United States, being confined to two species of *Sequoia*, the big trees (*S. gigantea* (Lindl.) Decne.) and the redwood (*S. sempervirens* (Lamb.) Endl.) of California and Oregon, and two species of *Taxodium*, baldcypress (*T. distichum* (L.) L. C. Rich.) and pondcypress

(*T. ascendens* Brongn.) of the southeastern states (not to be confused with the cypresses of the family Cupressaceae).

Stems and Roots.—The few remaining species of this family are trees, the best known of which are the sequoias of California. Some of these are 350 to 400 feet high and 20 to 30 feet in diameter—the largest forms of life the earth has ever known. The largest sequoias are estimated to be nearly 4,000 years old, having spent half their lifetime before the birth of Christ. A wondrous record of alternating prosperity and famine, as drought succeeded favorable climatic conditions, can be read in the varying widths of their annual rings. In *Taxodium* the growth of anchor roots, going on for centuries under so great a weight, has resulted in huge gnarled buttresses at the surface of the ground.

Leaves.—The leaves are linear or scale-like and alternate.

Strobili.—Both male and female strobili are borne on the same tree. There are several pollen sacs on the under side of each staminate scale and several ovules on the upper side of each ovuliferous scale. The female strobili develop into woody seed-bearing cones.

Seeds.—The seeds mature either the same season or the second season following fertilization. There are three to seven on each scale. A narrow wing extends as a margin all around each seed in *Sequoia* but is absent from the triangular seeds of *Taxodium*.

Economic Significance.—Were the trees of this family as abundant as those of Pinaceae, their value would be almost incalculable. Unfortunately, they are restricted to a small area. The redwood of California, *S. sempervirens*, furnishes lumber of unusual quality. It is reddish in color (except the sapwood, which is nearly white), evenly grained, light in weight, but rather strong, though brittle. It is rich in tannic acid and resists decay better than the woods of the Pinaceae. The lumber of *S. gigantea* is not of such good quality. There is, however, well-grounded sentiment against cutting these trees, for they are the last of the noblest race of trees the earth has produced. Furthermore, these great trees when cut shatter almost like glass and the waste is enormous—sometimes 60 to 90 per cent by the older methods of lumbering.

The baldcypress (*Taxodium*) is less restricted in its range than the sequoias, being found in the swampy regions of a dozen

of the southeastern states. Its habitat protects it somewhat from the woodman's axe, but it is slowly disappearing. The wood is of unusual quality, being heavier, harder, and stronger than that of the redwood and resisting decay even better. It is greatly sought for structural work in contact with the soil, where decay is most destructive, for greenhouse work, for staves, and indeed for a wide range of uses. In comparison with the sequoias of the Pacific coast, little effort is being made to conserve it.

3. CUPRESSACEAE. Cypress Family

The family Cupressaceae is rather small, containing but ten genera, widely distributed over both hemispheres.

Familiar Examples.—The commonest examples of the Cupressaceae are the cedars (*Thuja* and *Juniperus* spp.), junipers (*Juniperus* spp.), arborvitae (*Thuja* spp.), and cypresses (*Cupressus* sp.), but not the baldcypress (*Taxodium distichum* (L.) L. C. Rich.), which belongs to the Taxodiaceae.

Stems and Roots.—Many of the Cupressaceae are handsome shrubs, and some are large forest trees, the giant cedar reaching a height of 200 feet and a diameter of 15 feet. The tissues are resinous and in most species aromatic.

Leaves.—The leaves are small and linear, or, more often, scale-like and closely covering the twigs. They are evergreen, persisting usually from 3 to 5 years. They have an opposite or whorled arrangement on the stem, in which respect they differ from those of the Pinaceae and Taxodiaceae.

Strobili.—Some members are monoecious and others dioecious. The scales are few in number, each bearing either several pollen sacs or one to many ovules. In most genera the ovuliferous strobili develop into small woody cones, but in *Juniperus* the scales fuse into round blue or reddish fleshy bodies commonly called berries.

Seeds.—In the dry, woody cones the seeds generally produce narrow marginal wings. In the fleshy "berries" there are one to six seeds, which are wingless and usually angled.

Economic Significance.—The largest member of the family, the giant cedar (*Thuja plicata* D. Don), is a splendid forest tree growing extensively on the Pacific coast from Alaska to California. The others are smaller trees or shrubs. In general the wood is light in weight, soft and easily worked, but very durable.

It is, therefore, extensively used for shingles, fence posts, poles, ties, bridge work, and boats. Special uses are for cedar chests, where the aromatic wood acts as a repellent to moths, and for lead pencils, which require a soft, smooth-grained wood. Cedarwood oil is extracted for technical purposes.

Several of the smaller trees and shrubs are grown for ornamental purposes, but the red cedar (*Juniperus virginiana* L.), found extensively in the eastern United States, is an alternate host for the apple-rust fungus and is being replaced by other species that do not have this objectionable feature.

Order VII. GNETALES

The order Gnetales is very small. The living representatives belong to only three genera. Apparently originating as late as the Upper Cretaceous from unknown ancestors, the Gnetales have never been abundant or cosmopolitan. While they show some characters resembling angiosperms, their origin seems too late to permit their being ancestral to that class, and their naked ovules mark them definitely as gymnosperms.

Vegetative Structures.—The general appearance and habitat of the three genera are so different as not to suggest any relationship.

Ephedra with twenty-five species is a low, profusely branching shrub with small, opposite leaves and xerophytic characters. It is found mostly in southwestern United States and Mexico, but there are scattered patches in South America, Europe, and Africa.

Welwitschia, having only one species, is a very strange-looking plant, with a thick stem that scarcely rises above the surface of the ground and bears two great, opposite leaves, several feet long, that persist and grow slowly throughout the life of the plant, which may be more than a century. Its range is confined to the desert regions of southwest Africa.

Gnetum is made up of at least thirty-four species, mostly climbing vines 50 to 100 feet long, with large, oval, entire leaves at the tips, having netted veins. Different species are widely distributed throughout the jungles of South America, Africa, India, and the South Sea Islands, but none have been reported from North America, Europe, or Australia.

Numerous vessels are formed in the secondary xylem, but their

method of formation is somewhat different from that of the angiosperms.

Reproduction.—All three genera are dioecious, but some species show occasional monoecious plants and even bisexual strobili. The pollen grains form pollen tubes but no antherozoids. Archegonia, usually two, are found in the female gametophytes of *Ephedra* but not in those of *Welwitschia* or *Gnetum*. Pollination of all three takes place through a long micropylar tube. Fertilization is followed by the formation of embryos.

CHAPTER VII

FAMILIES OF DICOTYLEDONS

Of the two subclasses of angiosperms the subclass dicotyledons is much the larger, and it is correspondingly more important. While it is supposed to have originated before the monocotyledons, it has now reached a somewhat higher stage of development.

Origin.—That the first dicotyledons appeared in the early Mesozoic era, or perhaps the late Paleozoic, is generally conceded (see frontispiece). The oldest known fossils of this group are from the Lower Cretaceous rocks, but they show a degree of advancement that seems to justify us in believing that they had a long line of ancestors whose remains have not yet been found.

It is pretty generally agreed that the dicotyledons came from gymnosperms of a type somewhat different from any existing forms. The anatomy and histology of the stem, the spore formation, and the morphology of male and female gametophytes are all in harmony with this belief, if we make due allowance for advancement in structure by both gymnosperms and dicotyledons since the time when the former gave origin to the latter. In all likelihood both groups were considerably different at that time from any forms now existing; and an attempt to trace the connection through species now living or through a fragmentary fossil record is admittedly a treacherous undertaking. Some of the similarities noted may represent only parallel, or in some respects convergent, development of the two groups.

There are two general beliefs regarding the genetic connection of the groups of gymnosperms on the one hand and of dicotyledons on the other. Some hold the view that primitive Gnetales gave rise to primitive Amentiferae, now represented by willows, birches, etc. On this hypothesis the unisexual strobilus of the Gnetales is equivalent to the ament of the Amentiferae, the apetalous unisexual flower of the latter being primitively simple rather than simple by reduction. The Engler and Prantl system embodies this supposition. However, on purely theoretical

grounds Engler had predicated the existence of a large and varied group of herbaceous "protangiosperms" that gave origin to both the monocotyledons and the dicotyledons, the latter being polyphyletic. No fossil remains of such "protangiosperms" have ever been found, but the idea that the dicotyledons are polyphyletic seems to be gaining ground. Others maintain that the primitive Bennettitales or perhaps Cycadales gave rise to a

FIG. 25.—Two conceptions of the evolution of the flower from the strobilus. In the center is a strobilus. According to Engler, this contained only megaspores or microspores, and the entire strobilus developed into an ament, pistillate or staminate, each flower being apetalous and derived from a sporophyll of the ament. According to Bessey, the strobilus contained megaspores below and microspores above and developed into a single flower, the lower sporophylls becoming sterilized and forming sepals and petals, those next above forming stamens and the upper ones forming carpels. The axis shortened and became the strobiloid receptacle.

simple form of Ranales represented today by the Magnoliaceae, Ranunculaceae, etc. According to this belief the bisexual strobilus is homologous with a bisexual, symmetrical flower, the petals and sepals originating by a sterilization of the lower sporophylls. The system of Bessey is in harmony with this line of reasoning, which further maintains that apetalous and unisexual flowers have become so through a process of simplification.

It is beyond the scope of a beginner's textbook to deal adequately with all the families of flowering plants, and the student can best familiarize himself first with a limited number carefully selected from different parts of this great group of plants and

later extend his knowledge by more advanced study. To this end about sixty families have been selected for discussion in this chapter and the next. Some are chosen because of the large number of species that they contain; others, because of their economic importance; while a few, not so common or so important, have interesting peculiarities worthy of attention. All of those treated here are found in the United States, and most of them are widely distributed elsewhere.

The sequence in which these families are taken up follows the Besseyan system (proposed by Charles E. Bessey), which in the judgment of most American and some European taxonomists follows phylogeny most closely.

No attempt is made here to group the families into orders for two reasons. In the first place, some of the orders of the angiosperms are not clear-cut phylogenetic entities but are loosely and perhaps artificially associated families. As previously stated, most of our descriptive manuals of flowering plants either ignore the orders or name them without description. In the second place, a discussion of only sixty selected families would fail to bring out the significance of the orders.

Description.—The dicotyledons have some families entirely woody and others entirely herbaceous, but in most of the families both woody and herbaceous members can be found. In many families herbaceous species only are found in the temperate zones, but woody species also are found in the tropics and subtropics. Each seed contains two cotyledons, which may or may not rise above the ground during germination. In rare instances one cotyledon is absorbed in embryonic development, or more than two are formed. The fibrovascular bundles are characteristically arranged in a hollow cylinder, similar to that in the gymnosperms, with a cambium layer separating the tissues into bark and wood and forming, in woody perennials, annual rings of growth. The center is occupied by a pith that is never actually large, although it makes up a considerable proportion of the stem in the elderberries (*Sambucus* spp.), and it may be very tiny. With few exceptions the vascular bundles in the leaves form branched or netted veins. Dicotyledons are usually deciduous, the exceptions being a few evergreen shrubs and trees, probably derived from deciduous ancestors. In regions where the climate is uniform throughout the year, *i.e.*, not divided into winter and summer or

wet and dry, the distinction between deciduous and persistent leaves is not obvious.

1. MAGNOLIACEAE. Magnolia Family

$\mathrm{CA}^{x}\mathrm{CO}^{x}\mathrm{S}^{\infty}\mathrm{P}^{\infty}$

Some of the latest phylogenetic systems of classification, notably those of Bessey and of Hutchinson discussed in Chap. XI, rank the order Ranales, or what is sometimes spoken of as the "ranalean complex," as the most primitive of the angiosperms. In this basal group the family Magnoliaceae (given the rank of

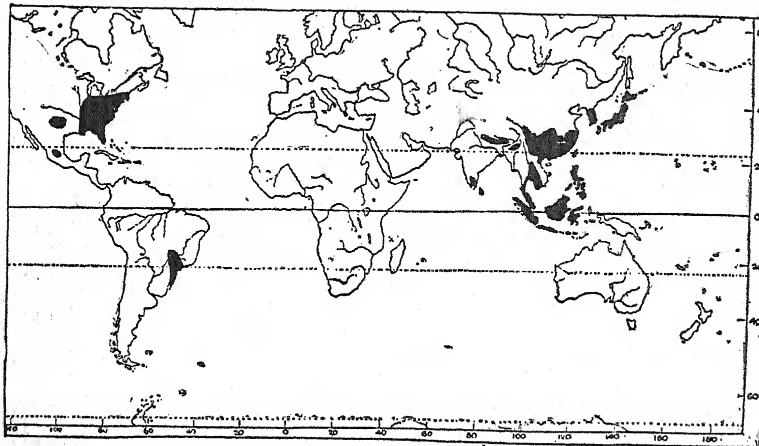


FIG. 26.—Distribution of Magnoliaceae. The complete isolation of members of this family, considered in conjunction with the anatomical and floral structures, indicates that it is of very great antiquity. (*After Hutchinson.*)

an order by Hutchinson) with its woody structure and large simple flowers stands as the most nearly ancestral form of any now in existence. No one supposes that the first angiosperms were like the magnolias of today; the belief is rather that the trees and shrubs of this family have departed less from the original form than have the members of other families.

This family at the present time is a rather small one consisting of only about 10 genera and 100 species. Their distribution is mostly subtropical and tropical, with a few remaining in the North Temperate Zone. There is evidence that the family originated near the Arctic Circle, perhaps in northern Canada, in the Cretaceous period or earlier, at a time when a subtropical climate obtained there, and that they then spread southward

and westward. Extremely abundant throughout most of the Cenozoic era, they might have continued to be a major unit of our forest flora but for the Glacial epoch which they were poorly equipped to resist. They are now recognized as beautiful survivors of a once noble race of trees.

Familiar Examples.—The best examples are the magnolias (*Magnolia* spp.) and the tuliptree (*Liriodendron Tulipifera* L.), which is the "yellow poplar" of lumbermen but is not related to the true poplars (*Populus* spp.) of the Salicaceae.

Stems and Roots.—The Magnoliaceae are all trees or shrubs. Since we have in the United States only two genera, those cited as examples above, this description will be limited to them.

The magnolias are best known in the southeastern United States where a half-dozen species are indigenous in moist, rich woods and have been freely transplanted to the old plantations and public grounds for the beauty of their flowers and foliage. Many have been transplanted to California, also. Most of them are small trees rarely exceeding 60 feet in height and often taking the form of large shrubs.

Of the tulip trees there are but two remaining species, one confined to the eastern United States and the other, so similar that it is sometimes classed as a variety, found exclusively in China. The tuliptree is of huge size, sometimes 200 feet high and 12 feet in diameter. Even in rather limited shade, the lower branches fall off when very young leaving a smooth, straight trunk almost to the top.

Leaves.—Magnolias bear alternate leaves of enormous size, sometimes as much as 30 inches long and 1 foot wide, generally entire, glossy-green above, thick, and leathery. They are deciduous in most species, but evergreen in *M. grandifolia* L. and somewhat so in *M. virginiana* L. Tuliptrees have large, thick, lobed or cleft, deciduous leaves. In both genera the leaves are petiolate, with prominent stipules that protect the leaf buds before expanding, and usually ensheath the stem at maturity.

Inflorescences and Flowers.—There is no definite inflorescence, the flowers being solitary but sometimes set rather close together near the tips of the branches. The flowers are the largest and most showy of any of the woody families. In some of the magnolias, *e.g.*, *M. Fraseri* Walt., they are as much as 10 inches in diameter. In the tuliptrees the flowers are cup-shaped

and 2 to 3 inches wide, depending on the degree of expansion. The perianth consists of six or nine separate parts, all showy, or the three outer ones green. They are arranged in whorls of three, the outer whorl being the calyx. The flowers are bisexual with many unicarpellate pistils arranged spirally on a cone-shaped receptacle and many stamens attached to this receptacle below the pistils.

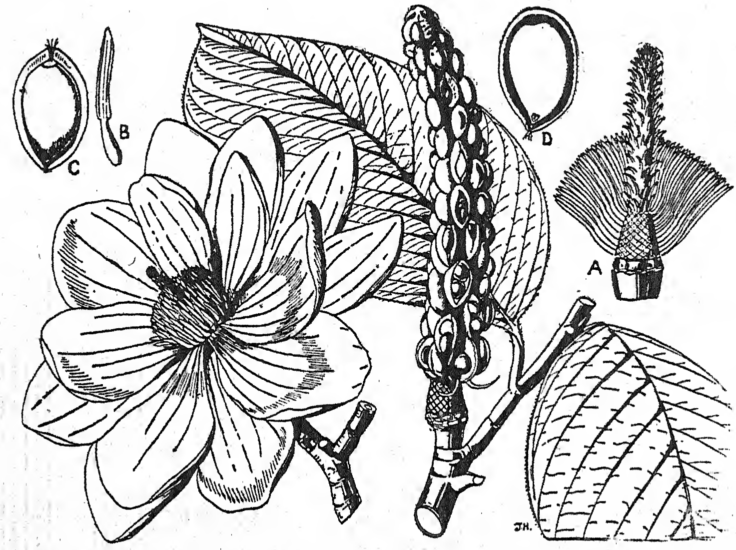


FIG. 27.—*Magnolia Campbellii* (Magnoliaceae). *A*, vertical section of flower with perianth removed. *B*, stamen. *C*, seed. *D*, section of seed. (*After Hooker*.)

Fruits and Seeds.—Each flower produces many fruits arranged on the receptacle to form a cone several inches long. The individual fruit is a tiny follicle in *Magnolia* and a samara in *Liriodendron*. In *Magnolia* the follicles dehisce and release one or two seeds which remain suspended for a time by slender threads. The very small embryo is embedded in endosperm.

Economic Significance.—The tuliptree is of considerable value for its lumber. In this country it practically never makes solid forests but is found mixed with other deciduous trees, although in parts of Europe it forms dense growths. For this reason the supply is limited even within its range. Because of the freedom of the trunks from branches the wood is clear of knots. While it

is not heavy or strong or beautiful in grain, there are few species that surpass it for certain purposes where a light, smooth, easily worked wood is required. Both genera, but especially the magnolias, are of surpassing beauty because of their big waxy-

FIG. 28.—*Liriodendron Tulipifera* (Magnoliaceae). Twig, bearing flower and leaf. (Three-fourths natural size.) (*Redrawn from Sargent.*)

white or yellow-tinted flowers and their great glossy leaves. It is unfortunate that their range and abundance are so restricted.

2. BERBERIDACEAE. Barberry Family

$$CA^6Co^6S^{6(4-9)}P^1$$

There are about 10 genera and 150 species of the Berberidaceae widely scattered throughout the Northern Hemisphere and South America but nowhere of sufficient abundance to form a major part of the flora.

Familiar Examples.—Common or European barberry (*Berberis vulgaris* L.), Japanese barberry (*Berberis Thunbergii* DC.), Oregongrape (*Mahonia* spp.), and wild mandrake or Mayapple (*Podophyllum peltatum* L.) are familiar examples.

Stems and Roots.—The species found in the United States are all shrubs or perennial herbs. In the woody genera the tissues of wood and bark are yellow.

Leaves.—In *Mahonia* the leaves are evergreen with sharp-toothed margins and are pinnately compound. In *Berberis*

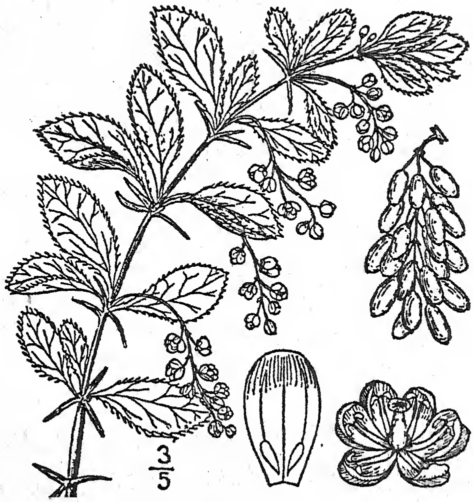


FIG. 29.—*Berberis vulgaris* (Berberidaceae). (*From Britton and Brown.*)

they are unifoliate, only the terminal leaflet developing and the others forming one to five thorns at the base of an apparently simple leaf. In all members of the family the leaves are alternate or basal.

Inflorescences and Flowers.—In *Berberis* and *Mahonia* the flowers are borne in racemes and are generally yellow. In other genera they may be solitary or variously clustered. The flowers are mostly small, bisexual, hypogynous, and regular, with distinct sepals and petals, the same number of stamens as petals, which may vary from four to nine, and one unicarpellate pistil.

Fruits and Seeds.—The fruit of many species is small and fleshy and is generally classed as a berry. In other species

it is a small capsule or an achene. The seed has a copious endosperm and a straight embryo.

Economic Significance.—The cultivated barberries introduced from the Orient have been extensively planted in the United States for hedges and ornamental shrubs. Their rapid growth, tough wood, protective thorns, and bright-red berries make them almost ideal for this purpose. The common form (*B. vulgaris* L.) is the more vigorous, and a horticultural variety of it has purple foliage. Unfortunately, *B. vulgaris* is attacked by the aecial stage of *Puccinia graminis* Pers., the fungus that causes stem rust of wheat, and the perpetuation of this disease in the colder climates is largely dependent on the barberry bush, which is necessary for a completion of the life cycle of the fungus. Since hope for control of this wheat rust in the northern United States lies in the extermination of the barberry, a vigorous national campaign is being carried on to that end. The Japanese barberry and all other species of the Berberidaceae found in America are practically resistant to the rust.

3. RANUNCULACEAE. Crowfoot or Buttercup Family

$$\mathrm{Ca}^{3-\infty}\,\mathrm{Co}^{0-\infty}\,\mathrm{S}^{\infty}\,\mathrm{P}^{x-\infty} \text{ or } \mathrm{Ca}^{2-5}\mathrm{Coz}^{2-5}\mathrm{S}^{\infty}\mathrm{P}^{x-\infty}$$

The family Ranunculaceae contains about 30 genera and 1,200 species of world-wide distribution. They are especially prevalent in temperate climates and some are found in arctic and alpine regions. The affinities of this family with the Magnoliaceae are easily seen and both are classed in the large and somewhat varied order Ranales.

Familiar Examples.—In the crowfoot family, familiar examples are the windflower (*Anemone* spp.), peony (*Paeonia* spp.), columbine (*Aquilegia* spp.), larkspur (*Delphinium* spp.), and virginsbower (*Clematis* spp.). Many of the "buttercups" belong to the genus *Ranunculus* of this family, but some are unrelated, belonging to Rosaceae and other families.

Stems and Roots.—The Ranunculaceae are nearly all herbaceous and mostly perennial, but in *Clematis* the stem is somewhat shrubby or takes the form of a woody vine, climbing by petioles that function as tendrils. In some genera, *Actaea*, *Cimicifuga*, and *Thalictrum*, the vascular system is not definitely cylindrical but the bundles are somewhat irregular like those of the mono-

cotyledons. There is a marked tendency for the development of rhizomes and fleshy roots in the perennial species.

Leaves.—Lack of stipules is the only characteristic feature of the leaves in this family, although in nearly all species they have an alternate arrangement. Generally they are large; but in

FIG. 30.—*Delphinium bicolor* (Ranunculaceae). This species is representative of the low larkspurs, which include *D. Menziesi*, *D. Geyeri*, and *D. Andersoni*. They are found in the plains and foothill regions, from the eastern slope of the Rocky Mountains westward. (One-third natural size.)

shape they vary from broad and entire, as in *Caltha natans* Pall., to decompound as in *Thalictrum*.

Inflorescences and Flowers.—There is no uniformity as to inflorescence. Many species produce solitary flowers, others irregular clusters. *Delphinium*, *Cimicifuga*, and *Aconitum* develop long racemes and *Thalictrum* has much-branched panicles.

The flowers are likewise variable. Generally they are bisexual, but in some species of *Thalictrum* they are unisexual and

FIG. 31.—*Delphinium cucullatum* (Ranunculaceae). The tall larkspurs which include *D. trolliifolium* and *D. barbeyi*, are found in sparsely wooded regions at rather high altitudes in the western mountains. (One-tenth natural size.)

dioecious. The sepals are distinct and vary in number from three to fifteen. In most species they are petal-like. The petals vary from three, or rarely none, to fifteen or more. In one branch of the family, including *Ranunculus* and *Paeonia*, they are alike, forming a symmetrical flower. In the other branch, including *Delphinium* and *Aconitum*, they are irregular, as are also the colored sepals. The stamens are numerous and distinct. The pistils vary in number from one to many and consist of separate carpels that may be slightly adherent, as in *Aquilegia* and *Delphinium*. All parts of the flower are hypogynous.

Fruits and Seeds.—The prevailing type of fruit is a follicle with many seeds. The different follicles may be adherent at the base to form a loose several-chambered capsule, or they may be distinct. If one-seeded, they produce achenes that are often plumed by a development of the style, as in *Clematis* and *Pulsatilla*. In *Actaea* and *Hydrastis* the fruit is a berry. The seed has a copious oily endosperm with a tiny straight embryo embedded near the apex.

Economic Significance.—The Ranunculaceae are best known for their flowers. Many of these, including peony, columbine, larkspur, and clematis, are extensively grown in dooryards. As a family it has a negative value for pasturage, for although wild peony and a few other members contribute a little to the food supply on the stock ranges of the west, this is offset in considerable measure by the losses from eating the poisonous larkspur, *Delphinium*, all species of which are deadly to cattle when eaten in quantity. Sheep and horses seem not to be affected. *Aconitum* is poisonous also, but is not so abundant and is less frequently eaten.

Several important drugs are obtained from this family. The most useful of these are aconite, hydrastis, cimicifugin, and staphisagria.

4. NYMPHAEACEAE. Waterlily Family

$$\mathrm{CA}^{3-6}\mathrm{Co}^{3-\infty}\mathrm{S}^{3-\infty}\mathrm{P}^{\underbrace{2-\infty}}$$

As the name indicates, this is a family of aquatic plants. There are eight genera and fifty-two species widely distributed over the earth, most abundant in the tropics but extending well into the temperate zones. They live in shallow lakes, ponds, and

slow-flowing streams. Some authorities believe that the Nymphaeaceae should be classed as two or more families.

Familiar Examples.—In the waters of the eastern United States the large, white, sweet-scented waterlily (*Nymphaea odorata* Ait.) is abundant, while in the west the yellow pond lily (*Nuphar polysepalum* Engelm.) replaces it. The American lotus (*Nelumbium luteum* Willd.) and the Indian lotus (*N. speciosum* Willd.) belong to this family also.

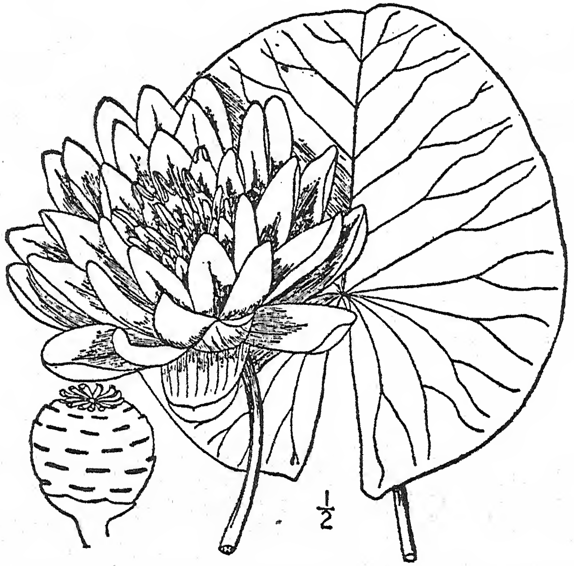


FIG. 32.—*Nymphaea odorata* (Nymphaeaceae). (*From Britton and Brown.*)

Stems and Roots.—In the mud at the bottom of the lake slender perennial roots are produced attached to numerous rootstocks.

Leaves.—Long leaf petioles arise from the rootstocks and produce broad blades that float on the surface of the water in most species. In the great *Victoria regia* of South America these leaves are of enormous size—3 to 6 feet in diameter with upturned margins. On these huge leaves water birds and animals often rest. In some genera the leaves are submerged and laciniate.

Inflorescences and Flowers.—The flowers are mostly solitary, large and showy, regular, and bisexual. In some species the calyx of three to six or more sepals is the conspicuous part of the flower,

the petals being reduced and the inner ones sometimes mistaken for stamens or staminodes. The white waterlily, however, has numerous, long, white petals. The many carpels are united into a broad expanded disk with short styles.

Fruits and Seeds.—The fruit is a capsule or berry of leathery texture, containing numerous seeds.

Economic Significance.—Nymphaeaceae are chiefly important for the beauty of their flowers. In the tropics these show great variety and brilliancy of color. A small lake of our white waterlilies with their broad floating leaves and large white flowers is a beautiful sight.

5. MALVACEAE. Mallow Family

$$\mathrm{C{\scriptstyle A}}^5\mathrm{Co}^5\mathrm{S}^{\underbrace{\infty}}\mathrm{P}^{\underbrace{5-\infty}}$$

The mallow family, sometimes known as the cotton family, contains about 50 genera and 1,000 species, many of which are confined to the tropics and subtropics. The family is represented in all parts of the world excepting the arctic zones.

Familiar Examples.—Cotton (*Gossypium* spp.), hollyhock (*Althaea rosea* Cav.), and hibiscus or rosemallow (*Hibiscus* spp.) are examples of the Malvaceae.

Stems and Roots.—The members of this family are mostly herbaceous, but in the tropics some shrubs and small trees are found. Usually they are sturdy, erect plants, but a few, as *Malva rotundifolia* L. and *Sida hederacea* Torr., are decumbent.

Leaves.—The leaves are generally large, broad, simple, and palmately veined, with petioles and deciduous stipules. They are alternately arranged on the stem.

Inflorescences and Flowers.—The flowers are either terminal or axillary, or sometimes in loose racemes. For the most part they are regular in shape, large, and showy. In many species each flower is subtended by three or more involucral bracts. With few exceptions the flowers are bisexual and hypogynous with a tendency to be 5-merous except for the large number of stamens. These are monadelphous, with their filaments united to form a conspicuous column encircling the pistil. Each pistil contains several carpels, five being the commonest number, but in different species they vary from one to many.

Fruits and Seeds.—The fruit is usually a capsule with each cavity containing one to several seeds. The seed has more or less endosperm and a straight or curved embryo. The seed coat is generally naked, but in a few species, notably in the genus *Gossypium*, it is densely tomentose. The hairs on the seeds furnish the cotton fiber of commerce. Each fiber or hair is the extension of an epidermal cell of the seed coat.

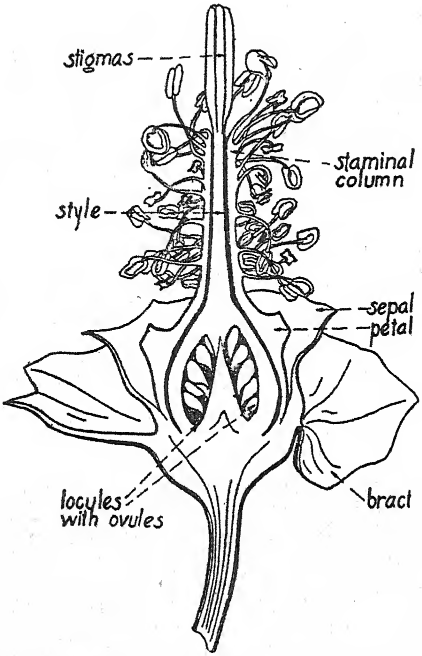


FIG. 33.—*Gossypium hirsutum* (Malvaceae). Longitudinal section of flower. (*After Robbins.*)

Economic Significance.—The cotton plant is the world's greatest source of textile fiber. Probably cotton is used for clothing and bedding more than are wool, silk, and linen combined. It is abundantly produced in most of the warmer countries, is relatively inexpensive, and is of better quality than any other commercial plant fiber excepting linen.

Much use is made of the oil from the seed as a substitute for lard, and of the remaining "oil cake" for stock feed. A few of the wild hollyhocks and mallows make good pasturage, but they

are not sufficiently abundant to give the family much forage value. The large size and variety of color found in the flowers of the hollyhock and many other species give them a prominent place in dooryards and flower gardens.

6. ULMACEAE. Elm Family

$$\text{C}\textsc{a}^{\underbrace{4-6}}\text{Co}^{0}\text{S}^{0-6}\text{P}^{(\underline{\overline{1:2}})-0}$$

The family Ulmaceae contains about 13 genera and 130 species represented in nearly all the warmer and temperate regions but not extending far into the north. Their geologic history extends back into the Cretaceous period but they are not nearly so well represented in those rocks as the other families of trees just discussed, and not being adapted to cold climates they were exterminated from vast areas during the Glacial epoch. To a limited extent these areas have been reforested.

Since the elms and the hackberries are the only members of importance in the United States, this account will be restricted to them.

Familiar Examples.—The elms (*Ulmus* spp.) and the hackberries (*Celtis* spp.) are common throughout most of the United States, and the planer tree or waterelm (*Planera aquatica* (Walt.) J. F. Gmel.) is found in the southeastern portion.

Stems and Roots.—The family is composed entirely of trees and shrubs, our white elm (*Ulmus americana* L.) being one of the largest of the deciduous trees. As a rule the trunks break up into branches a few feet from the ground and these long, graceful branches give a beautiful effect. The hackberries are rounder headed than the elms and not quite so graceful.

Leaves.—The leaves are simple and sharply serrate in the elms and some species of hackberry, with prominent veins. They are short-petioled or sessile, with an alternate arrangement on the stem. The stipules, if produced, are deciduous.

Inflorescences and Flowers.—The flowers are apetalous and borne in small clusters or racemes. They may be either bisexual or unisexual, and polygamous or monoecious, with a calyx of four to six sepals united or distinct. The pistil is bicarpellate, with two stigmas, one or two short styles, and a superior ovary.

Fruits and Seeds.—The fruit in the elms is a samara—a nutlet with a broad marginal wing. In the hackberries it is a very small drupe. There is no endosperm, and the embryo is straight.

FIG. 34.—*Ulmus fulva* (Ulmaceae). 1, branch with staminate and pistillate strobili. 2, staminate flower. 3, leaves 4, fruits. 5, twigs with flower buds and leaf buds. 6, leaf scar and lateral bud. 7, leaf scar. (*After Illick.*)

Economic Significance.—Interest in the Ulmaceae centers in the beauty of the elm trees and in less measure in that of the hackberries. Many make the mistake of trying to grow elms too far north and are disappointed in the results. A little use is made of the lumber for chairs and other furniture. It is fairly tough but not handsome and it does not resist exposure to the weather. When well seasoned it makes good fuel and is much used for that purpose.

7. GERANIACEAE. Geranium Family

$$\mathrm{Ca}^5\mathrm{Co}^5\mathrm{S}^{5-\infty}\mathrm{P}^{⑤}$$

There are in the Geraniaceae only about 11 genera and 650 species, found mostly in temperate climates and especially prevalent in South Africa.

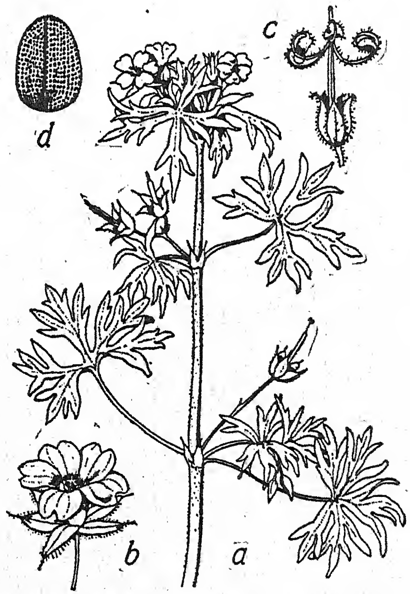


FIG. 35.—*Geranium dissectum* (Geraniaceae). *a*, floral branchlet. *b*, flower. *c*, dehiscent fruit. *d*, seed. (*After Jepson.*)

Familiar Examples.—Wild geranium or cranesbill (*Geranium* spp.), cultivated geraniums (*Pelargonium* spp.), and storksbill (*Erodium* spp.) are the only members of the geranium family commonly found in this country.

Stems and Roots.—The plants are all herbaceous except a few exotic half-shrubs. Our species are mostly perennial. Fleshy roots and rootstocks are common.

Leaves.—The leaves are generally deeply cleft or even compound. They are alternate or opposite, petiolate, usually stipulate, and in most species thickly covered with glandular hairs.

Inflorescences and Flowers.—Cymes are the commonest form of inflorescence, but umbels are found in *Pelargonium*. The flowers are showy, generally regular, but slightly irregular in *Pelargonium* and *Erodium*, bisexual, and 5-merous. Each flower is borne in a pair of small bracts. The sepals are distinct or united at the base. The petals are separate and hypogynous. There are usually five, ten, or fifteen stamens, some of which may be abortive, or, as in *Erodium*, reduced to staminodes. The pistil is usually 5-carpellate with one style and a superior ovary. The general effect of the flower, and indeed of the entire plant, is suggestive of the Rosaceae, but in Rosaceae the stamens are usually more numerous and the carpels numerous and distinct.

Fruits and Seeds.—The fruit is characteristically a beaked capsule with a persistent calyx on a long reflexed peduncle suggestive of the head and neck of a bird—hence the name cranesbill. In most species the capsule dehisces from the base upward. Each chamber contains but one seed, the other ovule having aborted. In *Erodium* a portion of the style remains attached to the seed as a hygroscopic awn. The seed contains little or no endosperm and an embryo that is usually curved.

Economic Significance.—Most of the Geraniaceae are palatable to livestock and make good forage. The flowers are handsome and abundant. Probably the common greenhouse geranium is grown in more homes than any other flower.

8. LINACEAE. Flax Family

$$\mathrm{Ca}^{\smile 5}\,\mathrm{Co}^{5}\,\mathrm{S}^{\smile 5}\,\mathrm{P}^{(\overline{\underline{2-5}})}$$

The family Linaceae is a rather small one, containing only 9 genera and about 150 species.

Familiar Examples.—The best examples are cultivated flax (*Linum usitatissimum* L.), wild perennial flax or Lewis' flax (*L. Lewisii* Pursh), and yellowflax (*Linum* spp.).

Stems and Roots.—The species found in the United States are all herbaceous, although a few foreign species are shrubby. The plants are taprooted.

Leaves.—For the most part the leaves in Linaceae are entire, narrow, sessile, and alternate. Stipules are absent or fugacious.

Inflorescences and Flowers.—The flowers are axillary or terminal on the upper branches, which may be so close as to give a corymbose or cymose effect. They are showy, bisexual,

FIG. 36.—*Linum usitatissimum* (Linaceae). (*From Britton and Brown.*)

regular, hypogynous, and mostly 5-merous. The sepals and petals are distinct. There are usually ten stamens in two whorls, the outer whorl being reduced to staminodes and the inner one united at the base. The pistil is composed of two to five united carpels, each of which has its cavity divided by a false partition giving the effect of four to ten carpels. Each apparent chamber encloses one ovule. The ovary is superior and the style number varies from one to five.

Fruits and Seeds.—The fruit is a capsule, which in flax is apparently ten-chambered. It normally contains ten seeds and

is slightly dehiscent along the lines of the true and false partitions. The seed contains a straight embryo and little or no endosperm.

Economic Significance.—The importance of Linaceae centers in one species, common flax, of which there are a number of varieties. This crop supplies us with linseed oil, for which there is no satisfactory substitute obtainable in sufficient quantity for the manufacture of house paint. It is extracted from the seed and the "oil cake," remaining after it has been expressed, is of value for stock feed. Our linen cloth is made from fiber removed from the bast of the bark by a process of "retting." It is wholly superior to all other fibers for certain purposes. Unfortunately, flax to be used for seed and that to be used for fiber must be grown and harvested under different conditions. In America most of the flax is raised for seed and the straw is discarded or fed to stock in times of famine. Most of our fine linen is produced in Europe.

The flowers of flax are beautiful when growing, but the petals fall quickly when they are picked.

9. RUTACEAE. Rue or Citrus Family

$$\text{C}\textsc{a}\,\underbrace{^{3-5}\text{C}\textsc{o}}^{3-5}\text{S}\underbrace{^{6-10}\text{P}}\,^{(\overline{2-5})}$$

The Rutaceae are little known in the United States, except through their cultivated forms, the citrus fruits. There are, all told, about 100 genera and 1,000 species, mostly tropical and subtropical, and especially prevalent in Africa and Australia. In this country we have but three native genera with one or two species each.

Familiar Examples.—Familiar examples of the rue family are orange, lemon, and grapefruit (*Citrus* spp.), pricklyash (*Zanthoxylum* spp.), and hoptree (*Ptelea trifoliata* L.).

Stems and Roots.—The Rutaceae are nearly all shrubs or small trees. In some species, such as lemon and pricklyash, the stems are protected by short, stout thorns. The bark is often fragrant.

Leaves.—The leaves show much variation. They are simple, or more often pinnately compound, and in the latter case some are apparently simple by reduction of leaflets to one. The arrangement on the stem is alternate, or less frequently opposite, and a considerable number of species, including the citrus fruits, are

evergreen. In many species there is an extensive production of aromatic glands in the leaves.

Inflorescences and Flowers.—The flowers are usually borne in cymes. They are typically 5-merous but multiples of three and four are common. They are regular or slightly irregular and are hypogynous, with a circular disk inside the whorl of stamens and bearing the pistil. The two to five carpels may be closely or loosely united.

Fruits and Seeds.—The fruit may be a samara, a capsule, or a berry; in the latter case it grows to great size in some of the citrus fruits. Each carpel produces from one to many seeds

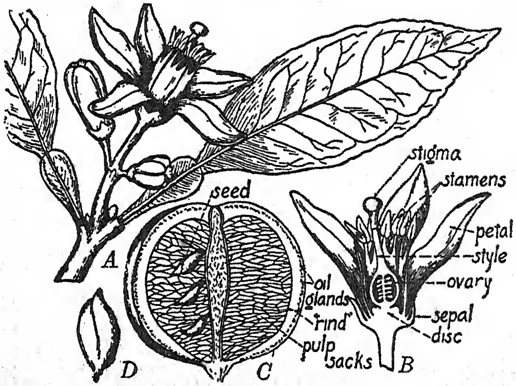


FIG. 37.—*Citrus aurantium* (Rutaceae.) *A*, flowering branch. *B*, lengthwise section of flower. *C*, lengthwise section of fruit. *D*, seed. (*After Wossidlo. From Robbins.*)

which may or may not contain endosperm, the embryo being straight or curved. In some species of *Citrus* more than one embryo develops in a seed, sometimes as many as thirteen, of which two or three may germinate.

Economic Significance.—Climatic conditions limit the growth of the Rutaceae in this country. The native species are interesting aromatic shrubs and trees of little value. The introduced citrus trees, however, are grown successfully in the Gulf States and California both for fruit and for ornament. So intensively are they grown in the limited areas that are suited to them that the family takes third place in fruit production. The good keeping and shipping qualities of oranges, lemons, and grapefruit, combined with their fine flavor and wholesomeness, ensure their continued prominence in the markets.

A few important drugs are extracted from the leaves and the rinds of the fruits, notably oil of citron, oil of bergamot, and oil of lemon.

10. EUPHORBIACEAE. Spurge Family

$$\mathrm{Ca}^{x-0}\mathrm{Co}^{x-0}\mathrm{S}^{x-\infty}\mathrm{P}\,(\overline{1:3})$$

The family Euphorbiaceae is a large and extremely variable one, containing about 250 genera and 4,000 species. They are of wide geographic distribution but are most abundant in the warmer climates, with few species extending beyond the Canadian border.

Familiar Examples.—Familiar examples of the spurge family are castorbean (*Ricinus communis* L.), crownofthorns (*Euphorbia splendens* Bojer.), snow-on-the-mountain (*Euphorbia marginata* Pursh), and poinsettia (*Euphorbia heterophylla* L.).

Stems and Roots.—Most of the family are herbaceous, but shrubs and trees are not uncommon in the tropics. The juice is acrid and in many species milky from the presence of starch, gums, and resins.

Leaves.—The leaves are mostly simple, with an alternate, opposite, or whorled arrangement, and in some species they have been reduced to spines.

Inflorescences and Flowers.—As would be expected in so large a family, there is considerable variety of inflorescence, but cymes are rather predominant. So great a variation is shown in the flowers that only general tendencies will here be indicated. Scarcely a statement can be made but will require exceptions. For the most part the flowers are 3-merous. Perhaps the most nearly constant character is the tricarpellate pistil. The tendency to reduction and specialization is very marked. This reaches its climax in *Chamaesyce* where the flowers have neither petals nor sepals and are unisexual, the staminate flower consisting of a receptacle and one stamen, and the pistillate flower a peduncle, a receptacle, and a pistil. In some species the leaves just under the flowers are white or red, giving the plant a striking appearance.

Fruits and Seeds.—The characteristic fruit is a three-chambered capsule, each chamber containing one seed, or the carpels may separate into three nutlets. The seed has a straight embryo and contains endosperm that is usually oily.

Economic Significance.—The Euphorbiaceae contribute but little to the food supply, although tapioca and other products of the fleshy root of *Manihot utilissima* Pohl. are worthy of mention. In general the herbage is unpalatable to livestock. Notwithstanding its deficiency in edible plants, this family is one of the

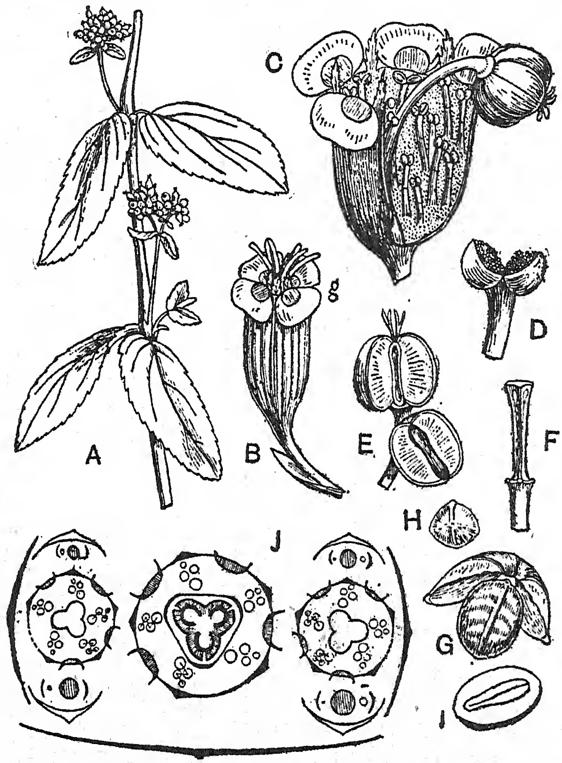


FIG. 38.—*Euphorbia hypericifolia* (Euphorbiaceae). *A*, inflorescences in clusters. *B* and *C*, single inflorescence (cyathium). *D*, stamen. *E*, fruit. *F*, axis of fruit. *G*, portion of fruit. *H*, seed (external). *I*, seed (internal). *J*, inflorescences and flowers of *E. peplis*. (*After Rendle.*)

most important to mankind because of the commercial and medicinal products extracted from the milky juice, the seeds, and the tissues of its numerous members. First in rank is caoutchouc, which, being manufactured into rubber, needs no introduction to any reader. It comes from the milky juice of several species of *Hevea*, *Mabea*, *Manihot*, and *Sapium*. Wood oil, artist's oil, tung oil, and other drying oils, some of which are even better

for paint than linseed oil, are extracted from the seeds of several species. Powerful drugs, especially those of a cathartic or irritant nature, are produced by many members. Probably no other plants have been used in the crude state for medicine so much as the Euphorbiaceae. Their properties have been discovered by natives the world over. In this country we now use castor oil, croton oil, cascarilla, hurta, and other products. A considerable number of deadly poisons are produced by exotic members of this family. Of these some are especially injurious through the stomach, others through wounds or when applied to the skin, and others are blinding to the eyes. It is not surprising, therefore, that they should have been used so much for warfare, murder, and suicide, and to kill fish, game, and insects.

Because of the brilliant color of the leaves surrounding the flowers a few species are used for ornamental purposes. The best known of these is the greenhouse poinsettia. The crownofthorns, with its weird, bare, spiny stems and gay floral bracts, is frequently grown as a house plant, and the castorbean is found in thousands of dooryards and flower gardens.

11. VIOLACEAE. Violet Family

$$\mathrm{C\scriptstyle{A}}^5\mathrm{C\scriptstyle{OZ}}^5(\mathrm{C\scriptstyle{O}}^5)\mathrm{S}\underset{\smile}{5}\mathrm{P}(\underline{\overline{1:3}})$$

The Violaceae include about 15 genera and 400 species, which are widely distributed.

Familiar Examples.—Violets (*Viola* spp.) and pansies (*V. tricolor* L.) are familiar examples.

Stems and Roots.—The representatives found in this country are all herbaceous and mostly perennial, but a few tropical forms are shrubby.

Leaves.—The leaves are simple and variously toothed, with a marked tendency to be cordate in form. They are petiolate with usually permanent stipules. In many species they are all basal, but in others alternately arranged.

Inflorescences and Flowers.—As a rule the flowers are solitary on long peduncles, but a few are racemose. In several of the genera the flowers are regular, but in *Viola*, the largest and best known genus, they are irregular with a spur on the basal petal. They are 5-merous except the pistil, which is tricarpellate. The parts outside the pistil are free or slightly connate. In some of

the violets two kinds of flowers are produced. Those that appear first are showy, as just described. They often fail to produce seed. These are followed by apetalous ones that are self-fertile and produce many seeds.

Fruits and Seeds.—The fruit is a three-chambered capsule that, in some species, discharges the seeds with considerable force. The seeds contain endosperm and a straight embryo.

Economic Significance.—The Violaceae are chiefly valued for their flowers, the violets and the pansies, both of which are found in nearly all climates, even beyond the Arctic Circle. There are at least 200 species of *Viola*, and through hybridization and selection hundreds of varieties have been produced. The violets are mostly in solid colors of many shades, but in the pansies broken colors are the rule and these are of innumerable patterns.

12. PAPAVERACEAE. Poppy Family

$$\text{Ca}^{2(3)}\text{Co}^{4-\infty}\text{S}^{\infty}\text{P}^{2-\infty}$$

Poppies, both wild and cultivated, are familiar to nearly everyone. The family contains 25 genera and about 150 species.

Familiar Examples.—Probably the large, red Oriental poppy (*Papaver orientale* S.) is the species most commonly grown in dooryards throughout the United States, but the yellow California poppy (*Escholtzia californica* Cham.) is found extensively in the far west. The opium poppy (*Papaver somniferum* L.) is widely cultivated in the warmer countries. The bleedingheart (*Dicentra spectabilis* Lem.), while differing in general appearance, belongs here, as does also the bloodroot (*Sanguinaria canadensis* L.).

Stems and Roots.—The Papaveraceae are mostly perennial herbs with a few annual species. The entire plant of some of the members of this family has a milky juice (latex), which varies in color from white to red.

Leaves.—The leaves are rather large, mostly alternate and simple, in some species lobed or cleft, and in a few species they are compound.

Inflorescences and Flowers.—The flowers of most poppies are solitary, but in the bleedingheart and some other species they are in racemes or panicles. They are quite variable. In the poppies they are large and regular with four to six showy petals. In others the petals are much smaller; *e.g.*, in the genus *Dicentra*,

which contains the bleedingheart and Dutchmans-breeches, the calyx is reduced to two small scale-like sepals and the petals are in two 2-merous whorls, the two inner petals more or less spurred at the base forming a hood over the stigma. The stamens vary from 6 to many. The carpels are united, with varying numbers in each ovary.

Fruits and Seeds.—The fruit is a capsule, usually opening at the top and containing many seeds.

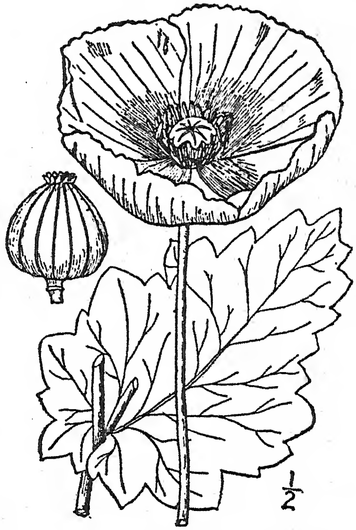


FIG. 39.—*Papaver somniferum* (Papaveraceae). (*From Britton and Brown.*)

Economic Significance.—Few plants are more significant to man, both for good and for evil, than the opium poppy. The opium is contained in the milky juice of the fruits and from it are derived a number of products, most important of which is morphine. When restricted to medical use they are of incomparable value, but unfortunately they are habit-forming, and their misuse is so great that it is debatable whether the plant is more of a blessing than a curse. From bloodroot the emetic alkaloid sanguinarine is obtained. The flowers of the poppies and bleedingheart are among the choicest.

13. CRUCIFERAE (BRASSICACEAE). Mustard Family

$$\mathrm{CA}^{4}\mathrm{Co}^{4(0)}\mathrm{S}^{4+2}\mathrm{P}^{2}$$

This important family contains about 200 genera and 2,000 species. They are widely distributed, especially in temperate climates. Most of them are mesophytic although some are semixerophytic. Foreign species are finding their way into this country, mostly through impurities in the seeds of crop plants, and many of those now here are becoming more thoroughly distributed as the virgin lands are brought under cultivation.

Familiar Examples.—Of the cultivated species, cabbage (*Brassica oleracea* var. *capitata* L.) and wallflower (*Cheiranthus*

Cheiri L.) are well known, while shepherdspurse (*Capsella Bursa-pastoris* (L.) Medic.) and the various wild mustards (*Brassica* spp., *Sisymbrium* spp., *Conringia* spp., etc.) are weeds that are common throughout the country.

Stems and Roots.—Nearly all the Cruciferae are herbaceous although a few shrubby species are known. They are usually taprooted and in some cultivated species the roots are fleshy. Both annuals and perennials are abundant and a considerable number are biennials.

Leaves.—The leaves are simple, pinnately cleft, or compound, and without stipules. The arrangement is usually alternate but in a few species is opposite.

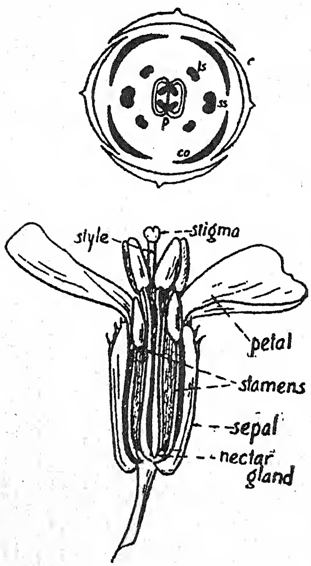


FIG. 40.—(Cruciferae). Floral diagram above—longitudinal section of flower below. (*After Robbins.*)

Inflorescences and Flowers.—In most Cruciferae the inflorescence is a raceme, but cymes are not uncommon. The flowers are small and regular with four petals (rarely none), and four sepals, the inner two usually narrower than the outer. There are six stamens in two whorls; the four inner ones are opposite the petals and have longer filaments than do the outer ones. The pistil is superior and composed of two carpels with one style and a stigma that is usually two-lobed but in some species is discoid. A false partition extends from one parietal placenta to the other, thus dividing the cavity into two chambers. The flowers are strictly hypogynous with all parts inserted on the receptacle.

Fruits and Seeds.—Two types of fruit are found, long cylindrical siliques and short broad silicles. Some of the latter (*e.g.*, in *Capsella*) have the partition through the short diameter and others (*e.g.*, in *Camelina*) through the long diameter.

The seeds are numerous, rounded, and without endosperm or with very little. The embryo is usually curved.

Economic Significance.—The family Cruciferae contains a few very useful members, contributing especially to the range of garden vegetables adapted to colder climates. Most of these are biennials, their value lying in the food stored the first year of growth. Considerable variation is found in the place of food storage. In turnip (*Brassica Rapa* L.), rutabaga (*B. Napobrassica* Mill.), radish (*Raphanus sativus* L.), and horseradish (*Armoracia rusticana* G. M. and S.) it is in the root. In kohlrabi (B. *caulorapa* Pasq.) it is in the stem. In cabbage (B. *oleracea capitata* L.) and Brussels sprouts (B. *oleracea gemmifera* Zenk.) it is in the leaves, and in cauliflower and broccoli (B. *oleracea botrytis* L.) it is in the inflorescence. In watercress (*Radicula Nasturtium-aquaticum* (L.) Brit. and Rend.) there is no localized food storage. Some of the mustards, including wild turnip (*B. campestris* L.), field mustard or charlock (*B. arvensis* (L.) Ktze.), and black mustard (*B. nigra* (L.) Koch) furnish considerable nectar that forms honey of fair quality. It is the more valuable from the fact that it is produced rather early, before the main honey flow in most sections comes on.

Because of the small size of the flowers most species of Cruciferae are not especially ornamental, but a considerable number, wallflower (*Cheiranthus Cheiri* L.), stock (*Mathiola* spp.), candytuft (*Iberis amara* L.), honesty (*Lunaria annua* L.), etc., have been improved to a point where they are handsome.

The table mustard of commerce is obtained from the seeds of black mustard (*B. nigra* (L.) Koch) and white mustard (*B. alba* (L.) Boiss.).

Owing to the acrid flavor of most members of the Cruciferae they have a limited forage value. The wild crucifers are quite generally rejected, although turnips, rutabagas, cabbage, and rape are grown to a limited extent for stock feed. None of the species of Cruciferae are distinctly poisonous.

Because of their prolific seeding, quick growth, and adaptation to a wide range of environmental conditions, many crucifers have become important weeds. Among the best known examples are shepherdspurse (*Capsella Bursa-pastoris* L.), field mustard (*B. arvensis* (L.) Ktze.), tumblemustard (*Sisymbrium altissimum* L.), falseflax (*Camelina sativa* (L.) Crantz), pennycress or fanweed (*Thlaspi arvense* L.), and one of the worst of all weeds in

some localities, whitetop (*Lepidium Draba* L.), which not only seeds heavily but is a perennial, forming rapidly spreading patches. For the most part the cruciferous weeds are pests of broken ground. Few of them can make headway in a well-established sod.

14. CARYOPHYLLACEAE. Pink Family

$$\mathrm{Ca}^{\underset{\smile}{4-5}}\mathrm{Co}^{4-5}\mathrm{S}^{8-10}\mathrm{P}^{(\boxed{2-5})}$$

In the Caryophyllaceae there are about 70 genera and 1,400 species of world-wide distribution but most numerous in the North Temperate Zone.

Familiar Examples.—Familiar examples are pinks (*Dianthus* spp.), carnation (*D. Caryophyllus* L.), sweetwilliam (*D. barbatus* L.), babysbreath (*Gypsophila paniculata* L.), and cow cockle (*Saponaria Vaccaria* L.).

FIG. 41.—*Agrostemma Githago* (Caryophyllaceae). (*From Britton and Brown.*)

Stems and Roots.—The Caryophyllaceae are all herbaceous (a few species slightly woody at the base), annual or perennial, and usually enlarged at the nodes. The annuals are mostly taprooted.

Leaves.—Almost without exception the leaves are opposite, rarely alternate near the top of the plant. They are entire, usually narrow and sessile, the pair at a node often united to each other around the stem. Stipules are not formed in most species.

Inflorescences and Flowers.—The inflorescence is usually cymose. The typical flower, as found in *Cerastium*, *Agrostemma*, and *Spergula*, for example, is regular, bisexual, and 5-merous, *i.e.*, with five sepals, five petals, ten stamens, and five carpels. By reduction, however, various modifications of this plan have developed. Thus in white campion (*Lychnis alba* Mil.) the

flowers are unisexual; in *Loeflingia* there are three to five stamens; in *Scopulophila* there are ten stamens, five of which are functional and five reduced to staminodes; and in *Sagina apetala* Ard. and *Achyronchia Cooperii* T. and G. the petals are absent or reduced to minute scales. Other modifications could be enumerated. This lack of uniformity in the flower need not indicate, however, that the family should be divided, for it is often a variation within the genus or even within the species, as in *Stellaria media* L. where the number of stamens varies from three to ten. As a rule the petals are separate and showy, the sepals are more or less united, and the ovary is superior with one cavity regardless of the number of carpels.

Fruits and Seeds.—The fruit is generally a one-chambered dehiscent capsule with seeds varying widely in number. In some species, however, it is a utricle enclosed in a persistent calyx. The embryo is usually wrapped around a central endosperm.

Economic Significance.—The Caryophyllaceae are chiefly valuable for their flowers. These are of many colors, solid or mixed, often of large size, and easily grown. The plants are unpalatable to livestock. Owing to their vigorous growth and free seeding some members are objectionable as weeds. These are especially chickweed (*Stellaria* spp. and *Cerastium* spp.), corncockle (*Agrostemma Githago* L.), and cow cockle (*Saponaria Vaccaria* L.).

15. CHENOPODIACEAE. Goosefoot or Beet Family

$$\mathrm{C_A}^{2-5}\mathrm{Co}^{0}\mathrm{S}^{2-5}\mathrm{P}\underline{\overline{(1:2-5)}}$$

The goosefoot family consists of about 75 genera and 500 species of world-wide distribution. A few are semixerophytic and many are halophytic, *i.e.*, especially adapted to growth in salty or alkali soil.

Familiar Examples.—Among the best known of the Chenopodiaceae are garden and sugar beets (*Beta vulgaris* L.), lambsquarters (*Chenopodium album* L.), Russianthistle (*Salsola pestifer* A. Nelson), greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), and summercypress (*Kochia scoparia* (L.) Schrad.).

Stems and Roots.—The Chenopodiaceae are mostly annuals, with some biennials and perennials, and a few shrubby species. While they vary considerably in texture, the majority are rather

succulent. As a rule they are taprooted and under cultivation the roots of some species become fleshy.

Leaves.—The leaves are simple and entire, or variously lobed, and without stipules. As a rule they are glabrous, but in *Chenopodium* especially they are covered with a glandular, mealy pubescence. The arrangement on the stem is alternate, or, in a few species, opposite. In some halophytic forms such as *Sarcobatus*, *Salsola*, *Suaeda*, *Allenrolfea*, and *Salicornia* they are much reduced in size, linear, or even scale-like. In such cases the stems perform largely the function of photosynthesis, and transpiration is slow, to correspond with the slow root absorption from the concentrated soil solution.

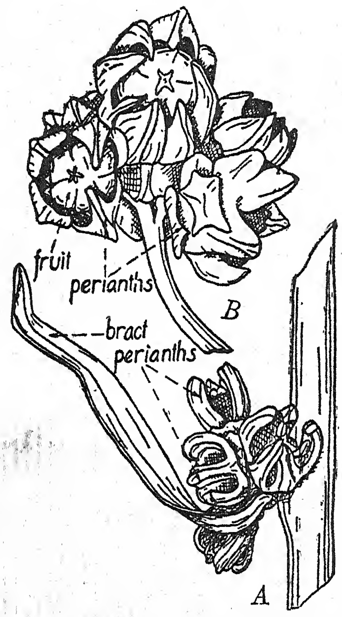


FIG. 42.—*Beta vulgaris* (Chenopodiaceae). *A*, axillary flower cluster. *B*, same fusing to form "seed ball." (*After Robbins*)

Inflorescences and Flowers.—The flowers are usually borne in small axillary clusters or rather dense spikes or panicles at the ends of the branches. They are apetalous and usually bisexual, but not infrequently unisexual and occasionally dioecious. The staminate flowers have a calyx of five or fewer sepals, usually more or less united. One stamen is formed opposite the middle of each sepal, or in some species the number is fewer than the sepals. In the pistillate flower the calyx is similar to that of the staminate flower, but it is lacking in certain genera, *e.g.*, *Atriplex*. It is free from the ovary or nearly so. The pistil is generally bicarpellate with one seed chamber, one ovule, and one to three styles and stigmas.

Fruits and Seeds.—The fruit proper, *i.e.*, the ripened ovary, is a utricle, a small, dry, one-seeded fruit with a pericarp formed by a persistent calyx, expanded receptacle, or bracteoles, or some combination of these. In the beet these appendages envelop several fruits in one irregular "seed ball." The genera vary as

to the presence or absence of endosperm, which, when present, is surrounded by the curved or coiled embryo.

Economic Significance.—The Chenopodiaceae are of considerable importance for food. Because of the succulent nature of the young stems and leaves, and the lack of objectionable flavor, this family surpasses all others for "greens." Spinach (*Spinacia oleracea* L.) and Swiss chard (*Beta vulgaris* var. *Cicla* L.) are the best examples, but garden and sugar beets and even wild forms such as lambsquarters and Russianthistle are much used and very good. The roots of garden beets as vegetables need no comment.

By far the most important member of the family is the sugar beet. As a source of "cane" sugar (sucrose) it is second only to sugar cane. Sugar beets do not yield nearly as heavily as sugar cane, but since they thrive in temperate climates while sugar cane is confined to the tropics and subtropics they make a distinct addition to the total output of this sugar, *i.e.*, about one-third.

The Chenopodiaceae have considerable forage value. None of the members is poisonous and a goodly number are abundant, palatable, and nutritious. Even Russianthistles are good forage plants when young, and they have been used for ensilage. The most valuable members on the stock ranges of the west are winterfat (*Eurotia* spp.) and the saltbushes (*Atriplex* spp.). The Chenopodiaceae are the more important because of their ready growth on lands so salty or so alkaline that most other kinds of vegetation cannot occupy them.

A few of this family are troublesome weeds, particularly Russianthistle in the semiarid parts of the west and lambsquarters throughout the country. Both these weeds are annuals, intruders on exposed soil only, and quite unable to compete with the grasses when the latter get started.

16. POLYGONACEAE. Buckwheat Family

$$\mathrm{CA}^{\underset{\smile}{2-6}}\mathrm{Co}^{0}\mathrm{S}^{2-9}\mathrm{P}^{(1:2-3)}$$

The family Polygonaceae is of medium size, having about 40 genera and 800 species. They are world-wide in distribution, the larger forms showing a preference for the warmer rather than the colder regions.

Familiar Examples.—Buckwheat (*Fagopyrum esculentum* Gaertn.), rhubarb or pieplant (*Rheum Rhaponticum* L.), and various kinds of dock (*Rumex* spp.) are familiar examples.

Stems and Roots.—Considerable variation can be found in the vegetative structure of the Polygonaceae. The majority are herbaceous, but a few in the subtropics and tropics are shrubby and even tree-like. Of the herbaceous members some are annuals, but more are perennials. A few are vines, but many more are erect. As a rule the stems are swollen at the nodes and in some the internodes are hollow. There is a strong tendency to the formation of red pigment in the epidermis.

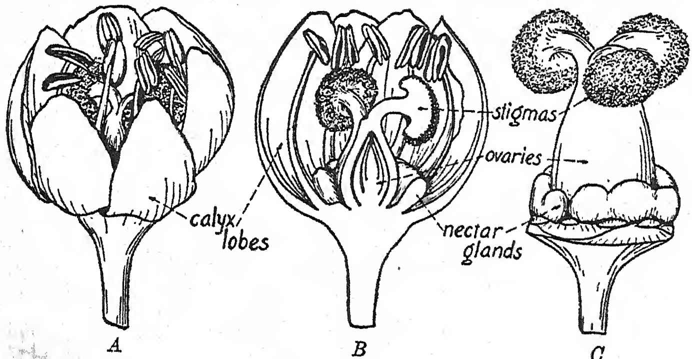


FIG. 43.—*Rheum Rhaponticum* (Polygonaceae). *A*, flower, external view. *B*, median longitudinal section. *C*, with perianth and stamens removed. (*After Lürssen*)

Leaves.—The leaves are entire or slightly lobed, rarely toothed or cleft. The arrangement on the stem is usually alternate, but sometimes opposite or whorled. The stipules are characteristic of the family with a few exceptions. They are broad and membranous and form a complete sheath (ocrea) around the stem.

Inflorescences and Flowers.—The inflorescences in the Polygonaceae are quite variable, spikes, racemes, panicles, umbels, and cymes being common. The flowers are apetalous, with a calyx of two to six sepals, which are united in some species. The pistil is tricarpellate, or occasionally bicarpellate as in *Oxyria*. It generally has one cavity and one ovule. The ovary is superior, with one to three short styles and usually three stigmas. While the flowers in most species are bisexual, in others they are unisexual and even dioecious. The sepals are often colored and

petal-like, white, red, or purple, giving a showy appearance to the inflorescence.

Fruits and Seeds.—The fruit is an achene, which in the usually tricarpellate species is three-angled. It may bear various appendages. In the docks the three inner sepals grow up around it forming three wings. In *Triplaris* the wings come from the three outer sepals. In *Coccolobis* the perianth becomes fleshy. The seed contains a large starchy endosperm and a straight to curved embryo.

Economic Significance.—From a food standpoint the Polygonaceae contain rather important members. Buckwheat is extensively raised in the eastern United States, Europe, and parts of Asia. It can be grown on very poor soil where few other crops are profitable. The large petioles of rhubarb make a world-wide substitute for fruit in pies, preserves, etc. A considerable number of species, notably buckwheat, secrete abundant nectar that makes honey of fair quality, though rather dark.

A few pernicious weeds belong to this family. Among these are wild buckwheat or bindweed (*Polygonum Convolvulus* L.), sheep sorrel (*Rumex Acetosella* L.), and wild begonia (*Rumex venosus* Pursh). For the most part the plants are unpalatable to stock though not poisonous.

17. SALICACEAE. Willow Family

$\mathrm{Ca}^0\mathrm{Co}^0\mathrm{S}^{1-x}$ or $\mathrm{Ca}^0\mathrm{Co}^0\mathrm{P}^{(\underline{1:2-4})}$

The Salicaceae contain but two genera—*Populus*, with about 30 species and several horticultural varieties, and *Salix* with over 190 species and many hybrids that make some sections of the genus difficult to classify. The family is a distinctly northern one, for, while representatives of both genera are found in the subtropics and even in the tropics, they are more numerous farther north and some species are found beyond the Arctic Circle and at the edges of glaciers high up in the mountains.

The race is an ancient one, both willow and poplar fossils being found in Cretaceous rocks. They were abundant throughout the Cenozoic era and withstood the glacial invasion of the Pleistocene epoch better than did most trees.

Familiar Examples.—The willows (*Salix* spp.) and the poplars (*Populus* spp.), some of which are also called cottonwoods, are the only examples.

Stems and Roots.—The poplars are all trees, the large ones more than 100 feet high and 6 feet in diameter. Some of the willows are trees as tall as the poplars, though not quite as large in diameter, but most of them are shrubs, some of the arctic and alpine species being only a few inches high. In general the Salicaceae make a rapid growth but are short-lived in comparison with the hardwood trees that make up the bulk of our deciduous forests.

Leaves.—The leaves are alternate and simple, with variously toothed margins and a shape varying from narrowly lanceolate in the willows to nearly circular in some of the poplars. Stipules are produced by nearly all species, but in some they are small and fugacious. In the willows the leaves are sessile or with short petioles, but in the poplars they have long petioles. The buds are large and scaly, and in certain species of *Populus* coated with a yellow, sticky aromatic secretion.

Inflorescences and Flowers.—All the family are dioecious (or by exception monoecious) with unisexual apetalous flowers borne in aments which appear in the spring in advance of the leaves. They are borne singly, as a rule, on the previous season's growth, in the axils of the leaf scars. On the willows the aments, especially the pistillate, tend to be erect, but on the poplars they are usually pendulous, especially the staminate.

The staminate aments vary in length from less than 1 inch in certain willows to 4 inches in some of the poplars. They produce many flowers, each subtended by a bract. Each flower consists simply of a small group of stamens set in a cup-shaped, often glandular disk. There is no recognizable perianth. Occasionally a bisexual flower or a pistillate flower develops in the staminate ament. The ament persists until the pollen is shed and then drops.

The pistillate ament contains many very simple pistillate flowers each of which is but a pistil in a concave disk without perianth. Each pistil is bicarpellate, with a short style and two to four stigmas. The ovules are numerous in a single chamber. Ordinarily the poplars are wind-pollinated and the willows insect-pollinated.

Fruits and Seeds.—The fruit is a small capsule dehiscing by two valves. The seeds are numerous, small, plumed, and without endosperm or nearly so. The embryo is straight. As soon

as the seeds are all or nearly all discharged, the aments that produced them drop.

Economic Significance.—The Salicaceae are somewhat exacting in their ecological requirements. They must have sun, and yet they do not thrive in hot climates. With sufficient water they grow in almost any kind of soil. For these reasons their distribution is unique. Where other trees can grow these do not, except scatteringly along forest streams. Where other trees find conditions uncongenial, on the banks of prairie streams and in cold marshes, there we find poplars and willows. They are therefore a distinct addition to the total of woody flora. The vast prairie regions of the semiarid west would be practically treeless but for the poplars.

The wood of the poplar is distinctly inferior in quality, but for fuel it is much better than no wood. It is little used for lumber, but the quaking aspen and some other species, because of their soft texture and whiteness, are extensively used for paper pulp, of which there is a shortage in this paper age. The willow wood is likewise of low grade for fuel, although it was formerly much used for charcoal. In strength, however, it is much superior to poplar, a fact which has given it some usefulness for cricket and baseball bats, implements, chairs, etc., where small pieces can be utilized. Its greatest use is for basketry where it has played a part since the dawn of civilization.

In many parts of the world where the finer shade trees thrive the poplars are regarded as inferior, but in many regions not so blest they are extensively planted for the shade and beauty which their rapid growth and dense foliage quickly provide. The plumes of the seed, commonly known as the cotton of cottonwoods, are so abundant in some species that they are distinctly objectionable. The trees are propagated by cuttings, and where these are taken from staminate trees only, this trouble is avoided.

The Salicaceae are not usually thought of as contributing much in the line of food, but in reality the shrubby willows furnish considerable browse for livestock in the mountainous regions of the west, and keep many deer and other wild animals from starvation when deep snows cover the grass. The poplars are said to furnish a supply of winter food for the beaver.

In sections where beekeeping is profitable the willows serve

the very useful function of supplying early nectar for brood rearing before most other honey plants come into bloom.

18. ERICACEAE. Heath Family

$$\mathrm{CA}^{4-5}\mathrm{Co}^{4-5}\mathrm{S}^{4-10}\mathrm{P}^{\underline{(2-5)}}$$

The Ericaceae as here treated include the Pyrolaceae, Monotropaceae, and Vacciniaceae of some authors. They have about 80 genera and 1,350 species, are world-wide in distribution, and are especially concentrated in Africa and southeastern Asia. They are commonly found as an undergrowth in forests, but some grow in the open.

Familiar Examples.—Well-known examples are trailing-arbutus (*Epigaea repens* L.), spicy or creeping wintergreen or checkerberry (*Gaultheria procumbens* L.), kinnikinnick or bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), laurel (*Kalmia* spp.), rhododendron (*Rhododendron* spp.), azalea (*Azalea* spp.), huckleberries (*Gaylussacia* spp.), blueberries and cranberries (*Vaccinium* spp.), and Indianpipe (*Monotropa uniflora* L.)

Stems and Roots.—This family is essentially shrubby, with a considerable number of woody vines and perennial herbs and a few trees.

Leaves.—The leaves are simple, often entire and sessile, exstipulate, and in most species evergreen. The leaf arrangement is commonly alternate but may be opposite or whorled.

Inflorescences and Flowers.—The inflorescence is varied, racemes, spikes, umbels, and solitary flowers being common. The flowers are polypetalous, or more often gamopetalous, and generally regular and bisexual. They are mostly 5-merous or 4-merous, with stamens double the number of petals and sepals. The insertion is hypogynous.

Fruits and Seeds.—The fruit is a capsule, berry, or drupe, with a straight embryo and endospermous seeds.

Economic Significance.—For flowering shrubs no family can compare with the Ericaceae. Their fragrant flowers, often in great clusters, and their glossy evergreen leaves give them a peculiar charm. They grow in great profusion out of doors, and are extensively raised under glass. Considerable honey is obtained from various members of the family, and sourwood (*Oxydendrum arboreum* (L.) DC.) is reputed to be the most valu-

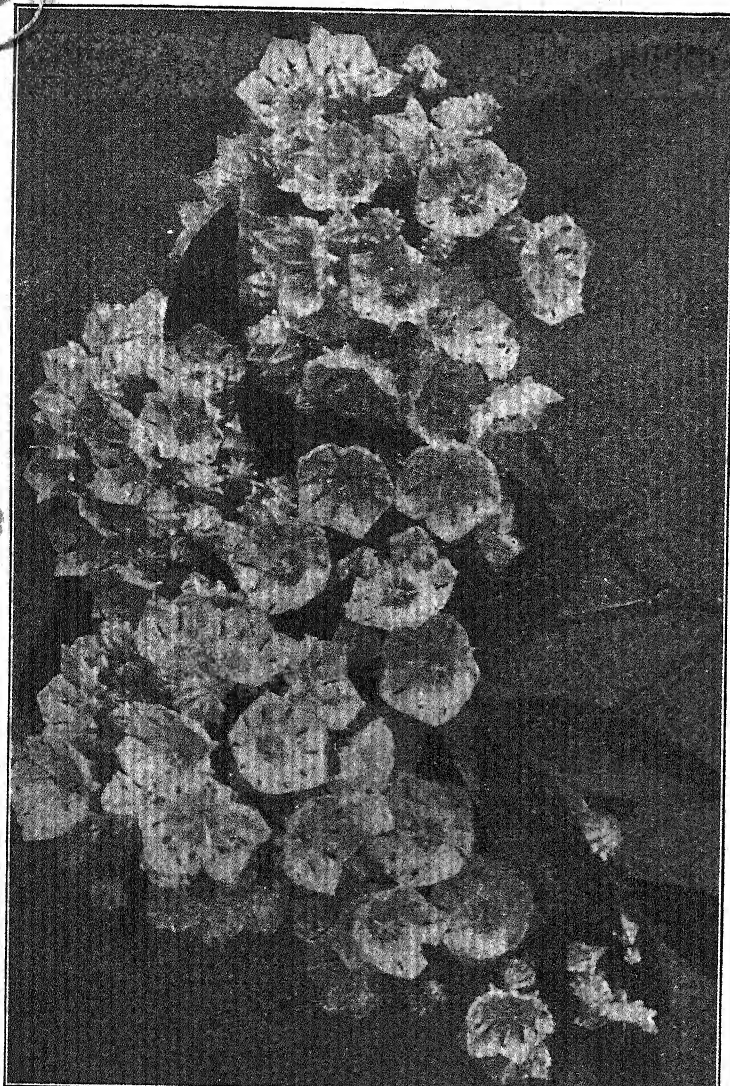


FIG. 44.—*Kalmia latifolia* (Ericaceae). Mountainlaurel. The laurels, of which there are many, are widely distributed throughout the wooded regions of the country, where they form a conspicuous portion of the undergrowth (Two-thirds natural size) (*After Dixon.*)

able honey-producing plant in the southeastern states, both for quantity and quality. The family has little forage value, but a considerable number of species are poisonous to livestock from the presence of andromedotoxin. The poisonous members include the laurels (*Kalmia latifolia* L., *K. angustifolia* L., *Ledum glandulosum* Nutt., *Leucothoe Davisiae* Torr., *Menziesia glabella*

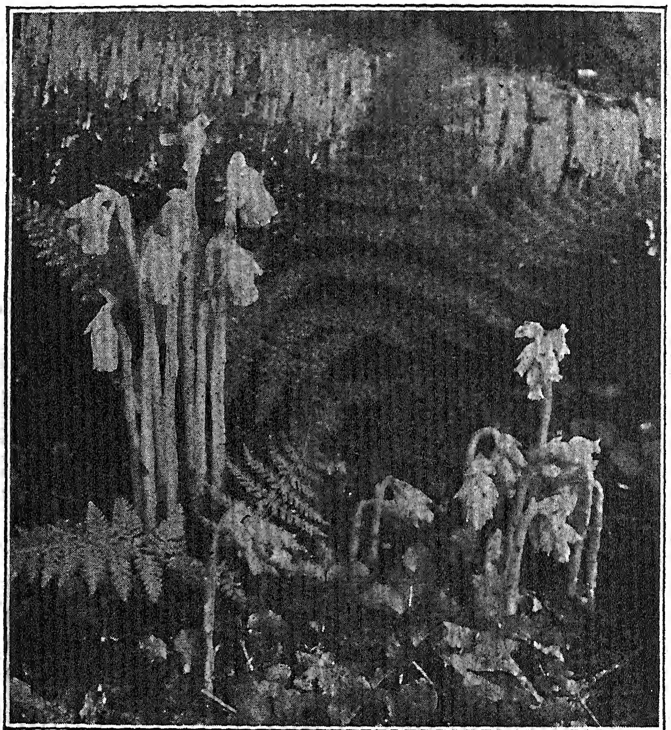


FIG. 45.—*Monotropa uniflora* (left), and *Hypopitys lanuginosa* (right), (Ericaceae). (*After Dixon.*)

Gray, *Rhododendron albiflorum* Hook., *R. occidentale* Gray) and probably other species. In general they are unpalatable, but if feed is scarce sheep may be forced to eat them with fatal results.

19. GENTIANACEAE. Gentian Family

$$\mathrm{C_A}\,\text{(4–5)}\;\overline{\overset{S^{4-5}}{\mathrm{C_O}\,\text{(4–5)}}}\;\mathrm{P}\,\text{(1:2)}$$

If the Menyanthaceae be excluded from the Gentianaceae, there remain in this family about 65 genera and 700 species.

They are of wide geographic distribution but are best known in temperate regions.

Familiar Examples.—The gentians (*Gentiana* spp.) and centaury (*Centaurium* spp.) are examples.

Stems and Roots.—The members of the Gentianaceae are practically all herbaceous, the perennial species often producing rhizomes. The juice of the plant is generally bitter to the taste.

FIG. 46.—*Gentiana crinita* (Gentianaceae). (*From Britton and Brown.*)

Leaves.—The leaves are opposite and exstipulate, and mostly entire and sessile. In a few saprophytic species they are much reduced and destitute of chlorophyll, or nearly so.

Inflorescences and Flowers.—In some species the flowers are terminal and solitary, but more commonly they are in cymes. The flowers are typically bisexual and 5-merous, but the sepals, petals, and stamens may be reduced to four, or increased to as many as twelve, and the pistil is bicarpellate. The calyx and corolla are regular, of more or less united segments. The stamens are attached to the throat of the corolla. The ovary is superior in most species.

Fruits and Seeds.—The fruit is generally a many-seeded, dehiscent capsule. The seed, as a rule, has a copious endosperm

with a small embryo, but exceptions are found in some saprophytic species.

Economic Significance.—Formerly much value was set upon the medicinal properties of various members of this family. Almost without exception they are so bitter that they are unpalatable to livestock. Probably their greatest value lies in the beauty and abundance of their flowers.

20. OLEACEAE. Olive Family

$$\mathrm{S}^{2-4}$$
$$\mathrm{CA}^{\smile 4}\overline{\mathrm{Co}^{0-4}\mathrm{P}}\textcircled{2}$$

The members of this family differ so much in appearance that the layman would not be likely to suspect that they are related. There are about 20 genera and 500 species. They are world-wide, in both temperate and subtropical regions.

Familiar Examples.—Growing wild or under cultivation in different parts of the United States are the ashes (*Fraxinus* spp.), lilacs (*Syringa* spp.), privets (*Ligustrum* spp.), jasmines (*Jasminum* spp.), and the olive (*Olea europaea* L.) introduced from southern Europe into California.

Stems and Roots.—The Oleaceae are for the most part composed of shrubs and small trees, but some species of *Fraxinus* reach a diameter of 2 feet.

Leaves.—In most species the leaves are opposite and simple, but in the ashes and a few others they are pinnately compound. In a few species they are persistent.

Inflorescences and Flowers.—The inflorescence is most commonly a panicle. The individual flowers are small, but handsome clusters may be formed, as in the lilac. In some species they are apetalous. They are commonly bisexual but sometimes are unisexual and dioecious. Sepals, petals, and stamens are commomly two to four. The ovary is composed of two united carpels.

Fruits and Seeds.—In *Fraxinus* the fruit is a winged achene (samara); in other genera it is a drupe or a few-seeded berry.

Economic Significance.—Many members of the family have ornamental value as shrubs and trees. The privets are especially desirable for hedges in climates where they thrive. Ash trees make very good hardwood lumber, competing with oak. Olives are produced in large quantity for their fruits and oil in southern Europe, California, and the Orient.

21. ASCLEPIADACEAE. Milkweed Family

$$\frac{S^5}{\text{Ca}⑤\,\overline{\text{Co}⑤}\,\text{P}②}$$

There are about 280 genera and 2,000 species of world-wide distribution but most abundant in the subtropics and tropics.

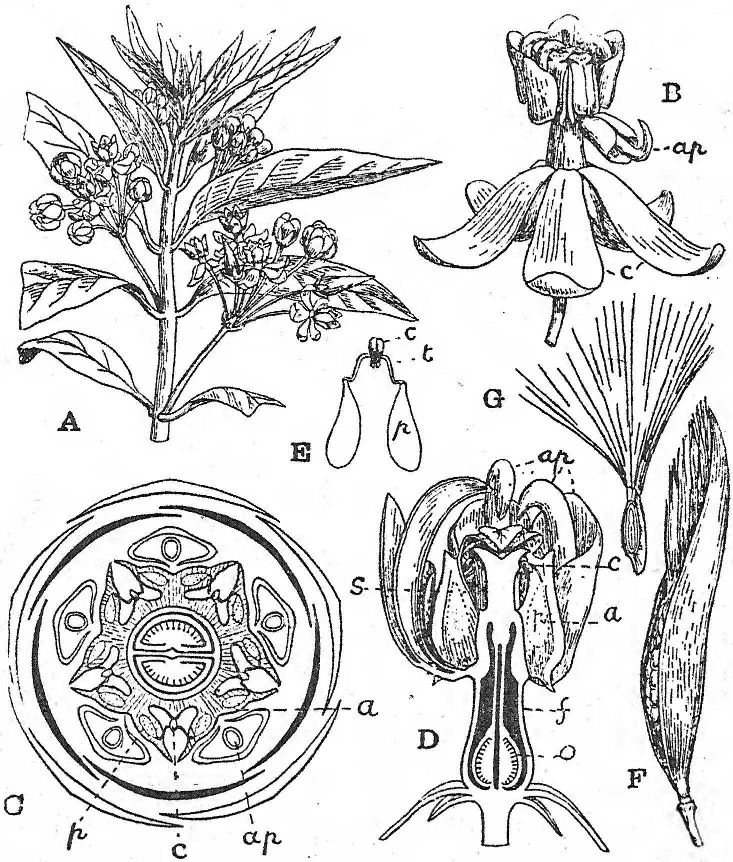


FIG. 47.—*Asclepias curassavica* (Asclepiadaceae). *A*, inflorescences. *B*, single flower. *C*, floral diagram. *D*, longitudinal section of flower. *E*, pollinium. *F*, fruit. *G*, seed. (*After Rendle.*)

Familiar Examples.—Milkweed or silkweed (*Asclepias* spp.), pleurisy-root (*A. tuberosa* L.), waxplant (*Hoya carnosa* R. Br.), and carrionflower (*Stapelia variegata* L.) are examples of the Asclepiadaceae.

Stems and Roots.—The species found in the United States are mostly perennial herbs, but in warmer climates shrubs and shrubby vines predominate and a few species become small trees. The fibrovascular bundles are bicollateral in type, and the plants

FIG. 48.—*Asclepias mexicana* (Asclepiadaceae). Mexican whorled milkweed. The milkweeds of this genus, several of which are poisonous, are widely distributed but are especially abundant on the open foothills of the western mountains. (One-half natural size.) (*After Marsh.*)

are filled with long, branching, laticiferous tubes which contain a starchy and albuminous milky juice. Rootstocks are common, and these may be long and slender for vegetative propagation, or fleshy and even tuberous for food storage.

Leaves.—The leaves are simple and generally entire, exstipulate, and opposite in most species.

Inflorescences and Flowers.—The inflorescence is mostly umbellate, but sometimes cymose or racemose. The flowers are rather small, regular, bisexual, and gamopetalous. They are 5-merous, except the pistil, which is bicarpellate with a superior ovary. The filaments attach to the base of the corolla and are often united to form a sheath or column around the pistil, the anthers being pressed close to the style. Each stamen bears, on the side away from the pistil, an appendage which enfolds the anther like a hood. Similar appendages are borne on the petals in some species. These appendages collectively make up the corona.

Fruits and Seeds.—The fruit is composed of two follicles, which may be close together or divergent. In *Asclepias* and some other genera they are large and pod-like. Each follicle contains many seeds, which commonly bear tufts of long, white, silky hair. The embryo is large and straight, and the endosperm hard and thin.

Economic Significance.—For the size of the family the Asclepiadaceae are relatively unimportant. They are unpalatable to livestock and a few species of *Asclepias* are rather troublesome as weeds. Recently a method has been found for separating the mass of hairs from the seeds and so treating them that they make good insulating material for lining jackets, etc.

22. CONVOLVULACEAE. Morningglory Family

$$\mathrm{S}^5$$
$$\mathrm{CA}\,\underset{\smile}{5}\,\overline{\mathrm{Co}\,\textcircled{5}}\,\mathrm{P}\,\textcircled{2}$$

About 45 genera and 1,000 species, most abundant in the tropics and subtropics but well known throughout the world.

Familiar Examples.—Familiar examples of the Convolvulaceae are morningglory (*Ipomoea* spp.), bindweed (*Convolvulus* spp.), some of which are often called morningglory, moonflower (*Calonyction aculeatum* House), sweetpotato (*Ipomoea Batatas* Lam.), and dodder (*Cuscuta* spp.).

Stems and Roots.—Most of the Convolvulaceae are twining herbaceous vines, but in the tropics some are shrubs, and a few are small trees. Often the vines are long and profuse, completely entangling the adjacent vegetation. A milky juice is not uncommon. The root system is very large. Sometimes the roots are long and slender, as in *Convolvulus arvensis* L., where they serve the purpose of vegetative propagation. Sometimes they are

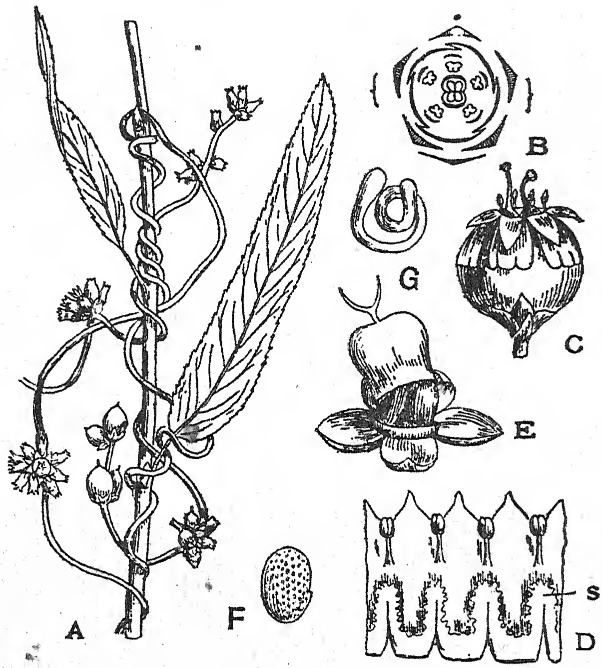


FIG. 49.—*Cuscuta* (Convolvulaceae). *A*, parasite on willow. *B*, floral diagram. *C*, fruit. *D*, corolla opened. *E*, fruit dehiscing. *F*, seed. *G*, embryo. (*A, E, and F after Peter. B, after Eichler. C, after Hooker. D, after Reichenbach. F, after Nees; arranged by Rendle.*)

thick and fleshy and of huge size, as in *Ipomoea pandurata* (L.) Meyer and *I. leptophylla* Torr., where they store great quantities of food. Thick tuberous rhizomes are found in *Convolvulus Scammonia*. The dodders are parasitic vines twining about various hosts, mostly herbaceous. Their color is very pale greenish, nearly white, reddish, or orange.

Leaves.—The leaves are simple, exstipulate, and alternately arranged. On the dodders they are reduced to scales.

Inflorescences and Flowers.—The flowers are solitary, or in small cymes. They are gamopetalous, regular, generally large and bell-shaped, and 5-merous with a bicarpellate or tricarpellate pistil. The calyx and corolla are inserted on the receptacle, and the stamens on the corolla tube, leaving the ovary free. There are from one to three long styles.

Fruits and Seeds.—The fruit is a capsule with two or three chambers, or, by false partitions, apparently twice the number. Each chamber encloses one or two seeds, each containing a more or less curved embryo and scanty endosperm.

Economic Significance.—The sweetpotato is one of our most important vegetables. The fleshy roots are produced in abundance, are rich in starch, and are of fine flavor. Of subtropical origin, they grow best in the south, although some varieties succeed in the middle states. The term "yam" is sometimes applied to the wetter fleshed varieties of sweetpotatoes, but it must be remembered that the true or Chinese yam is a monocotyledonous plant (*Dioscorea Batatas* Decne.).

The vigorously growing vines and large, many-colored flowers make the morningglories very desirable for trellises on porches, fences, etc. Unfortunately the flowers wither quickly when cut.

A few members are pernicious weeds, especially the small or European bindweed (*Convolvulus arvensis* L.). The family has very little forage value, although not poisonous. The dodders of alfalfa and clover reduce the yield somewhat and make trouble in haying by binding the plants together.

23. SOLANACEAE. Potato Family

$$\frac{S^5}{\mathrm{Ca}^{\underset{\smile}{5}}\mathrm{Co}^5\mathrm{P}\textcircled{2}} \text{ or } \frac{S^5}{\mathrm{Ca}^{\underset{\smile}{5}}\mathrm{Coz}^5\mathrm{P}\textcircled{2}}$$

The potato family is one of the best known, containing about 85 genera and 1,800 species. They are of wide distribution, especially abundant in the tropics and subtropics.

Familiar Examples.—Examples of the Solanaceae are potato (*Solanum tuberosum* L.), tomato (*Lycopersicon esculentum* Mill.), eggplant (*Solanum Melongena* L.), groundcherry (*Physalis* spp.), redpepper (*Capsicum frutescens* L.), and tobacco (*Nicotiana Tabacum* L.).

Stems and Roots.—The Solanaceae of the temperate zones are mostly herbaceous, but in the tropics many shrubby forms are

found and a few small trees. The production of underground tubers, such as those of the potato, is exceptional.

Leaves.—The leaves are mostly simple, but sometimes deeply cleft, and in a few species pinnately compound. They are exstipulate and usually alternate. They are evergreen in a few genera, as *Lycium*.

Inflorescences and Flowers.—The inflorescence is generally cymose or racemose, but solitary flowers are not unusual. The flowers are often large and showy, regular or nearly so, gamopetalous, and bisexual. There are five each of sepals, petals, and stamens, and a bicarpellate pistil with a superior ovary and, usually, a long style.

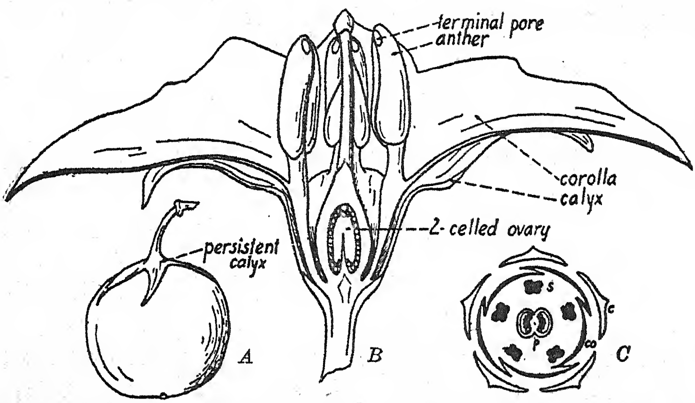


FIG. 50.—*Solanum tuberosum* (Solanaceae). *A*, fruit. *B*, longitudinal section of flower. *C*, floral diagram. (*After Robbins.*)

Fruits and Seeds.—The fruit is usually a berry, sometimes of very large size, as in tomato and eggplant. In those species where the pericarp does not develop a fleshy pulp, the fruit is a capsule. There are numerous seeds with fleshy endosperm and a curved or annular embryo. In some genera, such as *Physalis*, the persistent calyx develops a bladdery husk about the fruit.

Economic Significance.—The Solanaceae are of more than ordinary importance to the human race. They contribute heavily to the food supply through the potato, tomato, and eggplant. In the United States and Europe the potato ranks second to wheat. Tobacco is a major crop over large areas of the country, nearly 2 million acres being devoted to it, although its value is debatable. Powerful drugs, mostly of a narcotic nature,

and some of great value in medicine are characteristic of the family. The alkaloid solanine is found in greater or less quantity in many species, even in potatoes and tomatoes. Atropine, belladonna, capsicum, hyoscyamus, scopola, and stramonium are all obtained from this family. Some of the members, including the deadly nightshade (*Solanum nigrum* L.), are quite poisonous. Among the weeds belonging to this family, the jimsonweed (*Datura Stramonium* L.) is probably the most troublesome.

The large flowers and brightly colored berries make many species very attractive for flower gardens and dooryards. Among those worthy of mention are petunia (*Petunia hybrida* Vilm.), jessamine (*Cestrum* spp.), flowering tobacco (Nicotiana spp.), and Japanese matrimonyvine (*Lycium chinense* Mill.).

24. BORAGINACEAE. Borage Family

$$\mathrm{Ca}\,5\,\frac{\mathrm{S}^5}{\mathrm{Co}\,(5)}\,\mathrm{P}\,(2)$$

The Boraginaceae are prominently represented throughout the world with about 85 genera and 1,500 species.

Fig. 51.—*Cynoglossum officinale* (Boraginaceae). (*From Britton and Brown.*)

Familiar Examples.—Bluebells (*Mertensia* spp.), forgetmenot (*Myosotis* spp.), stickseed (*Lappula* spp.), and heliotrope (*Heliotropium peruvianum* L.) are examples of the borage family.

Leaves.—The leaves are simple, exstipulate, and usually narrow, sessile, and alternate, or the lower ones opposite and petiolate. In most species they are pubescent or even densely hairy.

Stems and Roots.—Most of the borage family are perennial herbs, a few being shrubs or trees.

Inflorescences and Flowers.—The inflorescence is characteristically a scorpioid cyme, which uncoils as the flowers open. The flowers are generally regular and bisexual. The calyx and corolla are tubular and often much elongated. The flowers are 5-merous, except the pistil, which is bicarpellate but usually with a four-lobed superior ovary. The stamens are inserted in the throat of the corolla.

Fruits and Seeds.—The fruit consists of four nutlets or drupelets, which may, however, remain united in a single body. Some species have little or no endosperm and others much. In some the embryo is straight and in others curved.

Economic Significance.—The flowers, which are generally bluish or purple, are often highly decorative. Many species of *Mertensia* are excellent forage plants and grow abundantly around springs and in marshy places in mountainous regions.

25. SCROPHULARIACEAE. Snapdragon or Figwort Family

$$\mathrm{C{\scriptstyle A}}\,\underbrace{5}\;\overline{\mathrm{C{\scriptstyle OZ}}\,\textcircled{5}}^{\,S^{2-5}}\;\mathrm{P}\,\textcircled{2}$$

Of the Scrophulariaceae there are about 205 genera and 2,600 species. They are widely distributed but most abundant in temperate zones.

Familiar Examples.—Examples are snapdragon (*Antirrhinum majus* L.), butter-and-eggs or toadflax (*Linaria vulgaris* Hill), beard-tongue (*Penstemon* spp.), monkeyflower (*Mimulus* spp), purple foxglove (*Digitalis purpurea* L.), mullein (*Verbascum Thapsus* L.), and Indian paintbrush or paintedcup (*Castilleja* spp.).

Stems and Roots.—The Scrophulariaceae are mostly herbaceous, but a few are shrubs or trees. The tendency to degenerate into a more or less complete parasite is found in about 15 per cent

of the genera and species. The method of parasitism is similiar to that found in the Orobanchaceae, *viz.*, the roots from the germinating seeds attack the roots of various host plants. As illustrating the different degrees of parasitism, *Gerardia flava* obtains very little of its food from the host and can live independently in its absence; *Pedicularis capitata* and *Odontites rubra* are half-parasites with small green leaves and terrestrial roots; *G. aphylla* takes most of its food from the host plant and has reduced

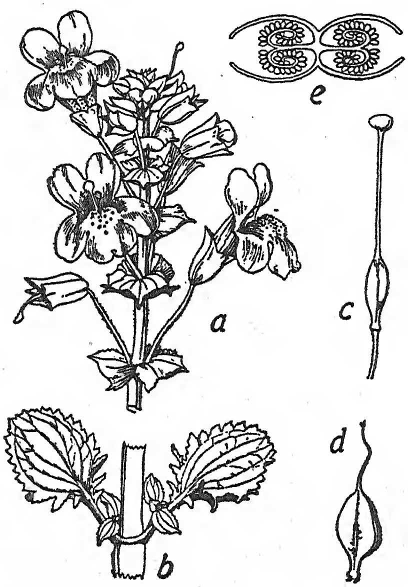


Fig. 52.—*Mimulus guttatus* (Scrophulariaceae). *a*, flowering branch. *b*, leaves. *c*, pistil. *d*, fruit (external). *e*, fruit (cross section.) (*After Jepson.*)

pale leaves; while species of *Harveya* and *Hyobanche* are wholly parasitic, destitute of chlorophyll, and bear scale-like leaves only.

Leaves.—The leaves are exstipulate and mostly simple. Their arrangement on the stem may be alternate, opposite, or whorled, and some of *Antirrhinum* have the lower leaves opposite and the upper leaves on the same stem spiral. The leaves on the parasitic species are more or less reduced and poorly supplied with chlorophyll.

Inflorescences and Flowers.—The inflorescences are variable, but racemes are very common. The flowers are bisexual, gamopetalous, and more or less irregular—usually two-lipped.

There are four or five united sepals, five united petals, two, four, or five stamens, and a bicarpellate pistil. The stamens are typically five, four of them in pairs of unequal length (didynamous), but some have been reduced to staminodes or lost. The ovary is superior, and the stamens are inserted on the corolla tube.

Fruits and Seeds.—The fruit is generally a capsule bearing many endospermous seeds, with straight or slightly curved embryos.

Economic Significance.—The importance of the Scrophulariaceae is rather limited. As forage plants most of the members are unpalatable and those that are relished do not recover well when cropped off. Their greatest value lies in their flowers, which show considerable variety of size, form, and color, and, as in the case of the Indian paintbrush, are supplemented by large colored bracts. Two rather important drugs are obtained from this family, digitalis and leptandrin. For so large a family not many are noxious weeds. Butter-and-eggs sometimes escapes from cultivation and forms persistent troublesome patches.

26. OROBANCHACEAE. Broomrape Family

$$\mathrm{C{\scriptstyle A}}\underbrace{^{4-5}}\overline{\dot{\mathrm{C}}\mathrm{{\scriptstyle OZ}}\underbrace{^{4-5}}}^{\;\mathrm{S}^{2+2}}\mathrm{P}(\overline{\underline{1:4}})$$

This is a small family of 11 genera and 200 species, which might almost be considered a subfamily or tribe of the Scrophulariaceae. Like most parasitic angiosperms they are not abundant over large areas but scattered widely. They are found most abundantly in the United States and Europe.

Parasitism in the flowering plants most commonly takes three forms: (1) In the mistletoes the seeds germinate on the bark of the host, which they penetrate directly. (2) In the dodders the seeds germinate in the soil and send up a twining stem that attacks the stem of the host, if a suitable one is within reach. (3) In the Orobanchaceae and some others the seeds germinate in the soil, forming seedlings the roots of which attack the roots of the host if one is available. In all cases success is dependent upon the right species of host being close to the seedling parasite.

Familiar Examples.—In this country beechdrops (*Epifagus virginana* L. Bart.) is parasitic on the roots of beech trees in the northeast. Cancer root (*Conopholis americana* (L.f.) Wallr.) is

FIG. 53.—*Orobanche minor* (Orobanchaceae). Parasite growing on clover (*After Strasburger.*)

found in oak forests of the east, and broomrape (*Orobanche* spp.), parasitic on clover and other plants, is widely distributed. However the majority of people in the United States have never chanced to see any of these plants.

Stems and Roots.—The Orobanchaceae are annual or perennial herbs, generally a few inches high, living parasitically on the roots of various host plants. Some are restricted in their parasitism to one species or genus of host plant, but others can attack a wider range. It has been shown that the seeds of some species of *Orobanche* at least will not germinate except when in contact with the roots of a suitable host. The root of the parasite becomes specialized into a haustorium that penetrates the bark, and the plant, nourished by its host, grows into the air and passes through its vegetative and reproductive stages. All parts of the plant are destitute of chlorophyll, or show mere traces, and are yellowish-white or brownish in color.

Leaves.—The leaves, like the stems, are white or yellowish, often with a tinge of red. They are small and scale-like and are only vestigial structures with little function.

Inflorescences and Flowers.—The flowers may be solitary, but more often they are in terminal racemes or spikes. There are four or five united sepals, and five petals united into an irregular, often two-lipped, tube. There are four stamens in pairs and often a fifth that is reduced to a staminode. Their insertion is perigynous. The pistil is bicarpellate with a superior ovary. In general the flower structure strongly suggests that of the Scrophulariaceae.

Fruits and Seeds.—The fruit is a small capsule with many tiny endospermous seeds in which the cotyledons are but slightly developed.

Economic Significance.—The family is interesting because of its parasitic nature but has little economic significance because of the scarcity of individual plants and the fact that most hosts suffer little harm.

27. LABIATAE. Mint Family

$$S^{2+2(2)}$$

$$\text{Ca}\,\textcircled{5}\,\overline{\text{Coz}\,\textcircled{5}}\,\text{P}\,\textcircled{2}$$

The mints are so distinctive in appearance and fragrance that they have been well recognized for centuries. There are about 170 genera and 3,000 species of world-wide distribution.

Familiar Examples.—Familiar examples are peppermint (*Mentha piperita* L.), catnip (*Nepeta Cataria* L.), hoarhound (*Marrubium vulgare* L.), thyme (*Thymus vulgaris* L.), sage (*Salvia* spp.)—not to be confused with "sagebrush" (*Artemisia* spp. of the family Compositae—skullcap (*Scutellaria* spp.), and coleus (*Coleus* spp.).

Stems and Roots.—The Labiatae are mostly herbaceous, but a considerable number of shrubs and a few small trees are found in the tropics. The stems of the herbaceous species are commonly square.

Leaves.—The leaves are simple, exstipulate, and opposite, or, in a few species, whorled. They are abundantly supplied with glands secreting volatile oils.

Inflorescences and Flowers.—The flowers are generally borne in small axillary cymes, which by their arrangement along the upper part of the stem often give the effect of a raceme. They are bisexual, gamopetalous, more or less irregular, and often two-lipped. There are four or five sepals and petals, and four or two stamens in pairs. If there are but two they are often supplemented by two staminodes. The pistil is bicarpellate with a superior ovary.

Fruits and Seeds.—The deeply two-lobed capsular fruit breaks up without true dehiscence into four nutlets. The seeds have little or no endosperm and the embryo is usually straight.

Economic Significance.—The Labiatae are chiefly valuable for their volatile oils, which are used for flavoring and for medicine. These are quite numerous and the list given above under familiar examples is but representative. Additional products of medicinal value are marrubium, hedeoma, and scutellaria. A few of the plants, such as coleus, are ornamental. The Labiatae quite generally yield nectar in abundance. The sages of California, especially the black sage (*Salvia mellifera* Greene), are among the heaviest producers, and the quality of the honey is excellent.

28. ROSACEAE. Rose Family

$$\text{CA}^{5(4-9)}\text{Co}^{5(4-9)}\text{S}^{1-\infty}\text{P}^{1-\infty}$$

The rose family is rather large, containing about 70 genera and 1,200 species. Its members are of world-wide distribution, only about one-fourth being found in the United States. They have considerable variation in morphological characters, as shown, for example, by the fruit of the rose and that of the raspberry. Some

authorities consider the Pomaceae and Drupaceae as tribes or subfamilies of the Rosaceae and claim that their separation is based on economic rather than scientific grounds, but the floral axis, gynoecium, and fruits in these families seem sufficiently different to justify separating them as is done here and by a num-

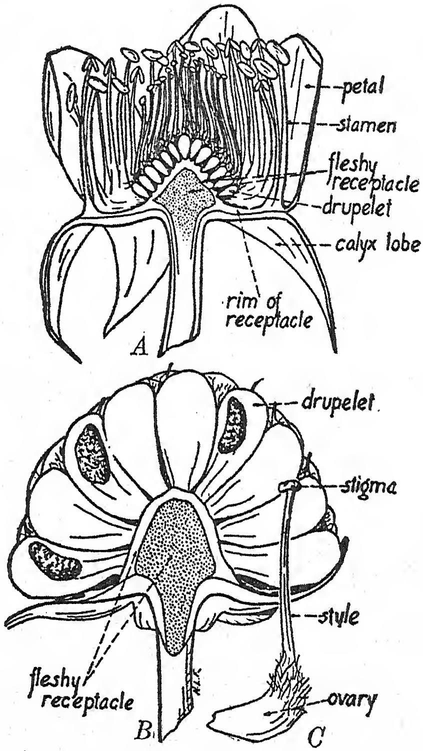


FIG. 54.—*Rubus strigosus* (Rosaceae). *A*, longitudinal section of flower. *B*, same of fruit. *C*, single pistil. (*After Robbins.*)

ber of other authorities. Certainly the relationship of the three families is close.

Familiar Examples.—Rose (*Rosa* spp.), raspberry (*Rubus* spp.), strawberry (*Fragaria* spp.), spirea (*Spiraea* spp.), and cinquefoil (*Potentilla* spp.), some species of which are called buttercups, are among the numerous examples of this family.

Stems and Roots.—The Rosaceae are mostly perennial herbs, but some species are shrubs and a few are trees. Many of the

shrubby forms are armed with spines which, in *Rosa* and *Rubus*, are protuberances of the cortex from both nodes and internodes. Trailing habit is not uncommon among both the herbaceous and the woody species.

Leaves.—Both simple and compound leaves are common, the latter usually pinnate. With rare exceptions the leaves bear stipules that are generally persistent. The arrangement on the stem is alternate. A few exotic species are evergreen.

Inflorescences and Flowers.—The inflorescence is variable, corymbs rather predominating. The flowers are usually bisexual and tend to be 5-merous, but numerous stamens and unicarpellate pistils are characteristic of certain genera such as *Geum*, *Potentilla*, *Fragaria*, and *Rubus*. For the most part the flowers are large, showy, and symmetrical, but in certain evergreen shrubs of South America they are somewhat irregular. In most species a central elevation of the receptacle is crowded with distinct unicarpellate pistils, but in the genus *Rosa* these are inside a cup-shaped hypanthium.

Fruits and Seeds.—The fruit proper, *i.e.*, the ripened pistil, is typically an achene, a small follicle, or a drupelet. In *Sieversia*, *Geum*, and some other genera the persistent style forms a plume on the achene. In *Potentilla* it is deciduous and the achene is naked. In *Fragaria* the achenes are partly embedded in the surface of a fleshy pulp formed by a development of the receptacle. In *Rubus* the carpels form as many drupelets attached to an elongated receptacle, thus producing an aggregate fruit. In *Spiraea* the pistils form dehiscent follicles. In *Rosa* the hypanthium surrounds the pistils and becomes fleshy with maturity, embedding the achenes, the whole forming a pome-like fruit, the well-known scarlet rose hip. The seed has a large, straight embryo with no endosperm.

Economic Significance.—As a source of fruit this family has only two or three rivals; indeed it may be considered the most important family for berries. Strawberries, raspberries, loganberries, blackberries, and blackcaps, considered in the aggregate, are of immense value. As food for livestock the family is of limited importance, for while mountain mahogany (*Cercocarpus* spp.), bitterbush (*Purshia tridentata* (Pursh.) DC.), and the wild roses make good browse, most herbaceous species are unpalatable. Many beautiful flowering shrubs belong to this

family, especially the roses and the spireas. Probably no other single genus of plants is as much cherished for its flowers as *Rosa*.

29. POMACEAE (MALACEAE). Apple Family

$$\frac{\mathrm{Ca}^5\mathrm{Co}^5\mathrm{S}^{1-\infty}}{\mathrm{P}^{(2-5)}}$$

Formerly a part of the Rosaceae, the Pomaceae are now on good authority given the rank of a distinct family that contains about 20 genera and 500 species of wide geographical distribution.

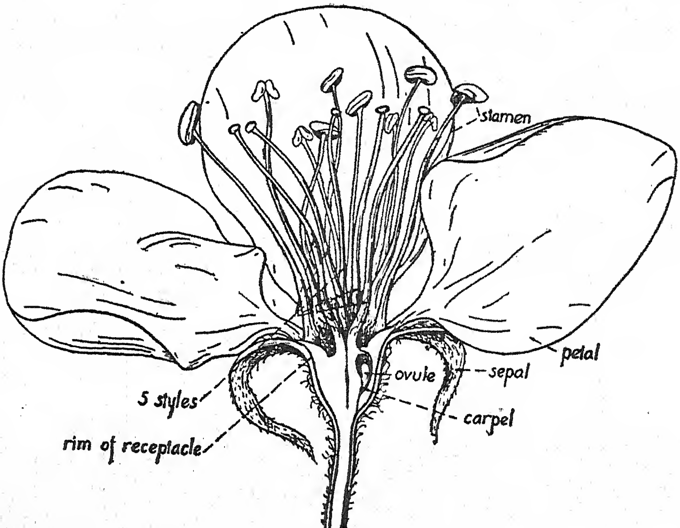


FIG. 55.—*Pyrus malus* (Pomaceae). Longitudinal section of flower. (*After Robbins.*)

Familiar Examples.—Well-known examples are apple and pear (*Pyrus* spp.), mountainash (*Sorbus* spp.), hawthorn (*Crataegus* spp.), and Juneberry or serviceberry (*Amelanchier* spp.).

Stems and Roots.—The Pomaceae are all shrubs or trees, some of the older apple trees reaching a diameter of 2 feet or more. The wood of all members is hard and strong. Most species of *Crataegus* are armed with stout thorns that are morphologically lateral branches.

Leaves.—In most genera the leaves are alternate, simple, serrate or dentate, and sometimes slightly lobed. They are provided with petioles and small deciduous stipules. *Sorbus*

has large pinnately compound leaves with well-developed stipules that persist until the leaves are fully expanded.

Inflorescences and Flowers.—As a rule the inflorescence is a compound raceme. The flowers are regular, bisexual and generally showy. The tendency is to be 5-merous but the stamens are rather numerous, and in some species the carpels are fewer than five—only one in some of the hawthorns. The carpels are firmly united into a single pistil that has an inferior ovary and one to five styles. The insertion is epigynous—sepals, petals, and stamens being attached to a well-developed hypanthium surrounding the ovary.

Fruits and Seeds.—The fruit is a pome that may be very large, as in apple and pear, or small and berry-like, as in mountain-ash, serviceberry, and hawthorn. In most genera the carpels are thin and hard, as in the core of an apple. There is no endosperm, the straight embryo entirely filling the seed.

Economic Significance.—No other family compares with *Pomaceae* in the extent of its fruit production. Literally hundreds of varieties of apples have been developed, with a wide range of colors, sizes, and flavors. They can be grown in different climates and soils, keep longer after picking than most fruits, and are more generally consumed than any other. Pears are important also but their poorer keeping qualities and limited range of flavors rank them far below apples in quantity consumption. Apple wood is used a little for tool handles and makes excellent fuel when available. The beauty of apple trees in bloom is worthy of mention, and considerable nectar is obtained from the flowers.

30. DRUPACEAE (AMYGDALACEAE). Plum Family

$$\frac{\mathrm{CA}^5\mathrm{Co}^5\mathrm{S}^{10-\infty}}{\mathrm{P}^1}$$

Like the Pomaceae, the plum family was set off from the older Rosaceae. It contains 3 genera and about 120 species.

Familiar Examples.—The best examples are peach (*Prunus persica* (L.) Stokes), almond (*P. communis* (L.) Fritsch.), apricot (*P. Armeniaca* L.), plum (*P.* spp.), cultivated cherry (*P.* spp.), and chokecherries (*P. virginiana* L. and *P. melanocarpa* (A. Nels.) Rydb.).

Stems and Roots.—All of the Drupaceae are shrubs or trees, some of the wild black cherries growing 100 feet high and 4 feet in diameter. The bark has a bitter taste due to traces of prussic acid and tannin. It also contains a glucoside, amygdalin, from which prussic acid is formed through the action of an enzyme, emulsin. When wounded the bark exudes a gum that is supposed to protect it to some extent.

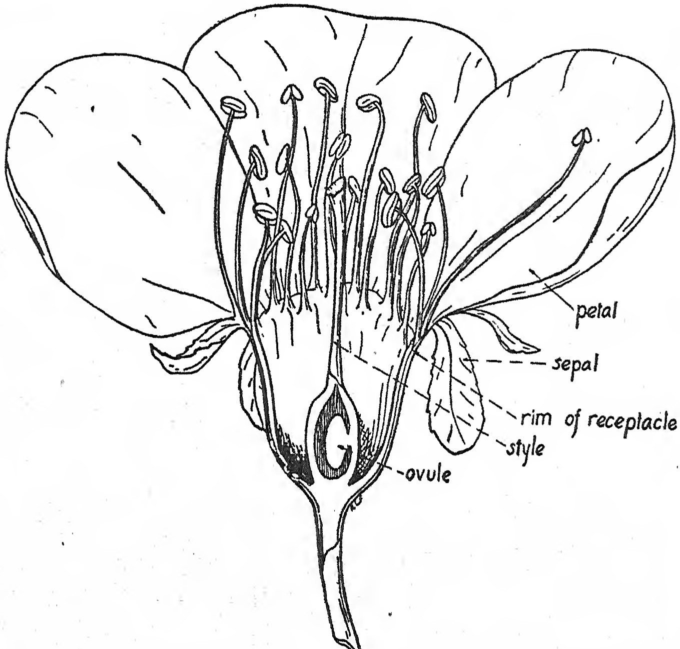


FIG. 56.—*Prunus cerasus* (Drupaceae). Longitudinal section of flower. (*After Robbins.*)

Leaves.—The leaves are alternate, simple, petiolate, serrate, and provided with small deciduous stipules. Usually a few conspicuous glands are found on the petioles. Like the bark the leaves contain prussic acid and amygdalin.

Inflorescences and Flowers.—The species vary in type of inflorescence. It may be umbellate, corymbose, or racemose, or the flowers may be solitary or in twos or threes. The flower is usually regular and complete, *i.e.*, bearing a full set of floral organs. The insertion is perigynous, leaving the unicarpellate

pistil free. The petal and sepal number is five and the stamen number is typically ten, fifteen, or twenty.

Fruits and Seeds.—The fruit is a drupe which is velvety in the peach and almond, but glabrous in most of the other species. The ovary wall develops into three layers, an outer epicarp or skin, a middle mesocarp or pulp, and an inner endocarp or stone. In the almond the mesocarp is leathery in texture. Although the pistil contains two ovules, usually only one forms a seed; the other fails to develop. In the almond two seeds are not uncommon. They contain prussic acid and amygdalin in amounts varying with the species—strong in bitter almond and apricot, but very little in the ordinary sweet almond. The seed is large but without endosperm. The seed coat is very thin, its function of protection being usurped by the endocarp of the fruit.

Economic Significance.—The Drupaceae rank second or third among the families in fruit production. Were peaches, cherries, and other stone fruits as good keepers after ripening as apples and oranges, they would probably be raised in greater abundance than either. Under the circumstances, the limiting factor in their production is the amount that can be consumed and preserved within a few weeks each season. Almonds are commonly classed as nuts although morphologically they are quite different. They are in such demand that the few regions of this country where the climate is suitable for their production are used to capacity.

In the eastern half of the United States where cherry grows wild and produces large trees, these are valuable for lumber. Cherry wood is reddish in color, rather heavy, moderately strong, and close grained. It is excellent for furniture and interior finishing and can be stained to imitate mahogany.

Some of the members are valuable for their prussic acid content. This may, however, be a source of danger, for children have been poisoned by eating the seeds of peaches and apricots, and when feed is scarce livestock will browse the leaves and twigs of wild cherry, a fact that has sometimes resulted in serious losses.

31. LEGUMINOSAE (FABACEAE) (PAPILIONACEAE). Pea Family

$$\mathrm{C{\small A}}^{5}\mathrm{C{\small OZ}}^{\underbrace{2}+2+1}\mathrm{S}^{\underbrace{9}+1}\mathrm{P}^{1}$$

This family is one of the largest and most important. The close relationship of its numerous members is shown by their pea-

like flowers, pod-like fruits, and compound leaves. They fall naturally into three subfamilies that some would call separate families, Mimosaceae, Caesalpinaceae, and Fabaceae or Papilionaceae. There are about 500 genera and 12,000 species, including large trees, shrubs, vines, perennial herbs, and annuals, of world-wide distribution. It is therefore the second largest family of the dicotyledons.

Fossil remains indicate that some woody members of the Leguminosae were in existence during the latter part of the Cretaceous period, but most of the species, perhaps all the herbaceous ones, are products of the latter part of the Cenozoic era and more recent times.

Familiar Examples.—Familiar examples are clovers (*Trifolium* spp.), alfalfa (*Medicago sativa* L.), sweetpea (*Lathyrus odoratus* L.), garden pea (*Pisum sativum* L.), soybean (*Glycine Max* Merr.), bean (*Phaseolus* spp.), lupine (*Lupinus* spp.), peanut (*Arachis hypogaea* L.), black locust (*Robinia Pseudo-acacia* L.), and many others.

Stems and Roots.—The Leguminosae are predominantly herbaceous, but there are many shrubs, woody vines, and trees. The largest member of the family is the black locust, which not infrequently reaches a height of 80 feet and a diameter of 2 to 3 feet.

The root system in the species that are perennial herbs is generally large and deep, *e.g.*, in alfalfa. The roots of most species are commonly attacked by bacteria belonging to the genus *Rhizobium*. These enter through the root hairs and cause what appears to be a diseased condition, in that certain cells are killed and inhabited by the bacteria, and other cells are stimulated to abnormal multiplication that results in the formation of many tiny galls or nodules. This localized injury is more than offset, however, by the benefit the host receives from the bacteria, which are among the few species that have the power of using the inert nitrogen of the air and uniting it with other elements to form compounds usable for food by the leguminous host.

Leaves.—With few exceptions the leaves are compound, more often pinnate than palmate, and possessed of permanent stipules. Some of those leaves that appear to be simple are, in reality, unifoliolate. The arrangement on the stem is alternate. In several genera, such as *Lathyrus*, *Pisum*, and *Vicia*, the terminal leaflet

and sometimes others are reduced to a tendril. Movements of the leaflets or the leaves are fairly common. In *Trifolium* and *Phaseolus*, for example, the leaflets take a vertical position as darkness comes on. In the sensitive plants, *Mimosa pudica* L. and *Aeschynomene virginica* (L.) B.S.P., the petiole droops and the leaflets fold together when the latter are touched. In *Desmodium gyrans* DC., the telegraph plant, two lateral leaflets wave up and down periodically without external stimulus.

Inflorescences and Flowers.—The most common inflorescence in the Leguminosae is a raceme, which in some cases, as the clovers, is shortened to such an extent that it is often spoken of as a head.

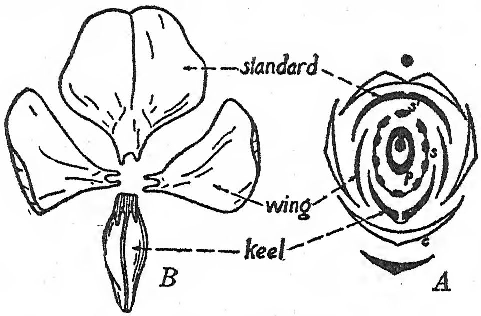


FIG. 57.—*A*, *Vicia faba*. *B*, *Lathyrus odoratus* (Leguminosae). (*A*, *after Eichler; B, after Bergen and Caldwell.*)

The flower is quite characteristic in most species. Generally it is complete and hypogynous or perigynous. The five or four sepals are more or less united. The five petals are unlike, forming an irregular flower with bilateral symmetry. The large upper petal is called the standard. On either side are two others, similar to each other, called the wings. Below these, and more or less enclosed by them, is the keel, which consists of two united petals, the others being distinct. In *Amorpha* the wings and keel are wanting, and in several species of *Lespedeza* some of the flowers are apetalous. There are generally ten stamens, which in most species have their filaments united into one or two series. The pistil contains a single carpel with a superior ovary. A considerable number of species show highly specialized devices for insect pollination. In this respect the family almost approaches the Orchidaceae.

Fruits and Seeds.—Each flower develops a single true pod, often called a legume. Commonly the pod is dehiscent, but not infrequently it develops into a special indehiscent hooked structure for seed distribution by animals. In *Glycyrrhiza* the pod is short and unsegmented and bears well-developed hooks. In *Desmodium*, *Hedysarum*, and other genera of the same tribe the pods are divided transversely into easily separated segments covered with very fine hooks, and contributing to that heterogeneous group of fruits known as "beggars' lice." In *Medicago* the pods are small, spirally coiled, and either hooked or reticulated. The peanut (*Arachis hypogaca* L.) fruits in a very special way. As soon as the flowers in the axils of the lower leaves are fertilized they lose their petals and the peduncle turns downward, forcing the ovary into the soft soil. When thus buried it develops into the well-known peanut. If it fails to get buried because it started too far above ground or the ground was too hard, the ovary withers and dies. The seeds of Papilionaceae contain a large curved embryo, with little or no endosperm.

Economic Significance.—The Leguminosae rank second only to Gramineae in value to mankind. Probably a wider range of usefulness is found here than in any other family. Much significance lies in the fact that the Leguminosae are highly nitrogenous in all their tissues. For this reason they supplement well the foods and feeds obtained from the Gramineae, which are largely of a carbohydrate nature. The special food value of peas and beans is well known, and the fine flavor and oil and protein content of peanuts make them usable in many forms. No other plant except timothy yields so much hay as clover and alfalfa, and the pasture value of the legumes ranks above all others except the grasses. The soybean is grown extensively not only for food but for oil and raw material for plastics.

Even if the legumes were wholly unpalatable, they would be extensively raised, however, because of their value to the soil. For centuries it has been known that crops of this character enrich the soil although other crops impoverish it. The explanation has been given on page 152. The decaying roots and stubble bring much avaliable nitrogen into the soil even though the stems and leaves are removed for hay. It is indeed rare good fortune that after the harvesting of an unusually valuable crop, such as clover or alfalfa, the land is left in much better condition for

other crops. Man's benefit by the alliance between leguminous plants and the bacteria that inhabit their roots is incalculable.

As a source of honey no other family compares with the Papilionaceae—indeed in many states the yield from this family

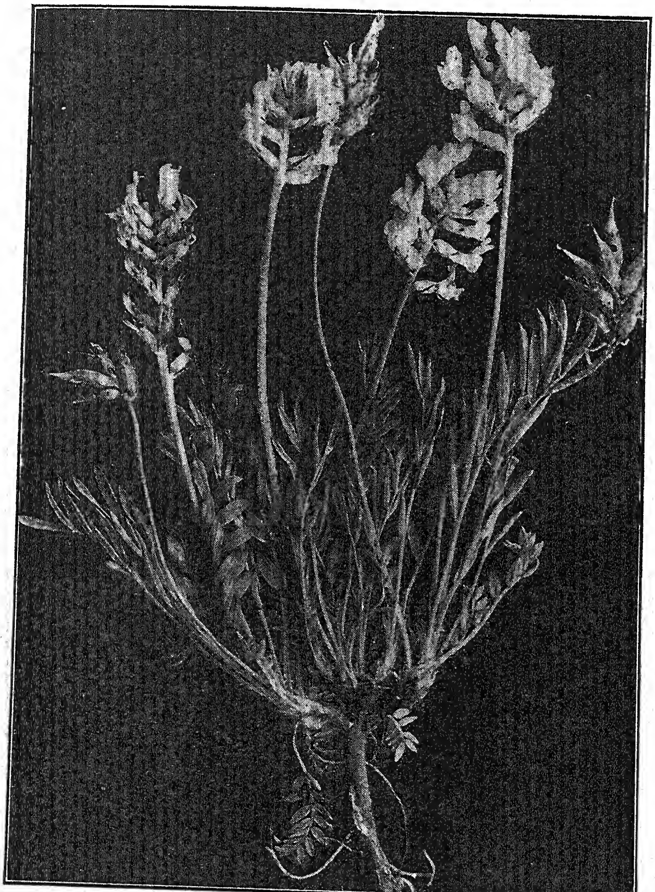


FIG. 58.—*Oxytropis Lamberti* (Leguminosae). White or stemless loco. This plant is found in the open country from the Rocky Mountains eastward to Minnesota. (One-half natural size.)

exceeds that from all other families combined. In white and alsike clovers, alfalfa, and sweetclover we have four of the greatest honey producers, and the quality is of the best.

In esthetic value this family ranks high. It includes myriads

of beautiful wild flowers, and sweetpeas and black locust illustrate the cultivated forms.

From no other family are so many official drugs obtained. These include licorice, hematoxylin, tragacanth, senna, and physostigmine.

Two important groups of stock poisoning plants are found in this family, *viz.*, the locoes and the lupines. The locoes include *Oxytropis Lamberti* Pursh and a few species of *Astragalus*, notably

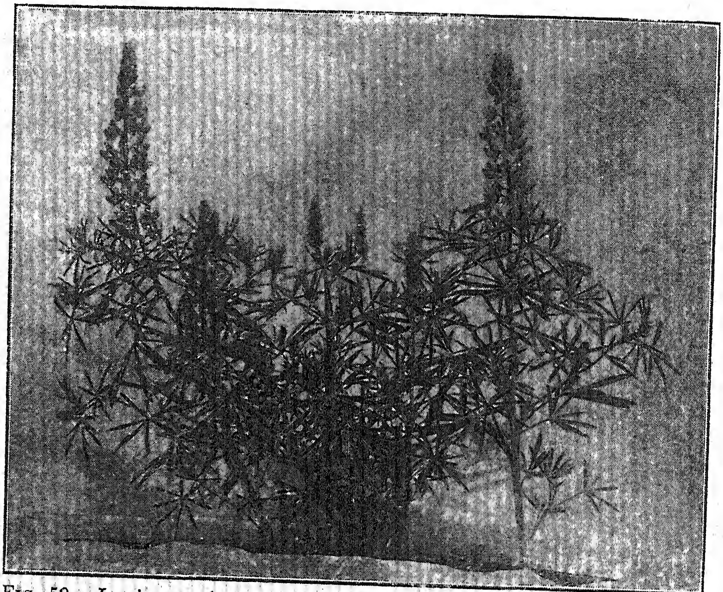


FIG. 59.—*Lupinus sericeus* (Leguminosae). The lupines, of which there are many species, are found at nearly all altitudes throughout the western half of the United States. (One-fourth natural size.)

A. mollissimus Torr. The poisonous principle in these plants is unknown, and its effects are evident only after continuous feeding for weeks or months. Loco poisoning causes heavy losses among horses, cattle, sheep, and goats. There is increasing evidence, however, that other maladies in domestic animals are erroneously attributed to loco weeds. The lupines cause acute poisoning, especially in sheep. The poisonous principle has not been isolated, but the losses are mostly from eating young pods containing seeds. The mature pods are so freely dehiscent that ripe seeds rarely are eaten in quantity.

For so large a family, the Leguminosae are remarkably free from members that are classed as noxious weeds. This is in part because some that have the persistent habit of weeds are so freely eaten by livestock that they are thought of as forage plants rather than weeds. In many places white, alsike, and sweet clovers abound, but although "plants out of place" they are not classified as weeds. A few, such as wild licorice or buffalo bur (*Glycyrrhiza lepidota* Pursh), are obnoxious.

32. SAXIFRAGACEAE. Saxifrage Family

$$\mathrm{CA}^{5(4)}\mathrm{CO}^{5(4)}\mathrm{S}^{5-10}\mathrm{P}(\boxed{1-4})$$

The family Saxifragaceae is a somewhat variable one, especially if it be made to include the Grossulariaceae as one of its tribes. Without the currants and gooseberries, as here considered, it

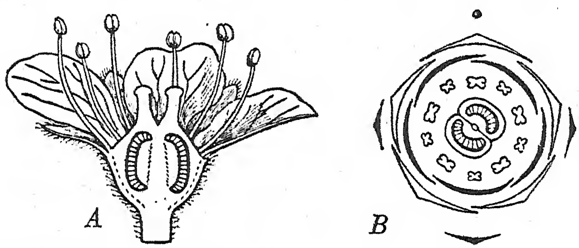


FIG. 60.—*Saxifraga granulata* (Saxifragaceae). *A*, longitudinal section of flower. *B*, floral diagram. (*A, after Warming; B, after Eichler.*)

contains about 75 genera and 800 species, found chiefly in temperate zones and even extending into the arctic regions.

Familiar Examples.—The saxifrages (*Saxifraga* spp.), hydrangea (*Hydrangea* spp.), and syringa or mockorange (*Philadelphus* spp.) are among the best known examples.

Stems and Roots.—The members of this family are mostly perennial herbs or shrubs, but a very few are trees. There is a considerable tendency to vegetative propagation through rootstocks, runners, and bulbils.

Leaves.—The leaves are quite variable. They are mostly spiral, simple, exstipulate, and deciduous, but exceptions are found in all these characters. In the herbaceous forms there is a tendency to produce masses of basal leaves, with slender, leafless stems.

Inflorescences and Flowers.—There is no uniformity or general tendency in the inflorescence. The flowers are mostly bisex-

ual and regular. The typical flower is 5-merous, but the carpels are often reduced, two being a common number. They are separate or loosely united. The stamen number is often twice that of the petals, which are usually five but are lacking in a few species. The insertion is usually hypogynous or perigynous, but every gradation between may be found.

Fruits and Seeds.—The fruit is generally a capsule or follicle, producing numerous seeds with abundant endosperm and a straight embryo.

Economic Significance.—Except for a few ornamental plants, the family is of little importance. Most of the species are unpalatable to livestock and sparsely produced. It is of considerable botanical interest because of its plasticity and consequent variability.

33. GROSSULARIACEAE. Gooseberry Family

$$\frac{\mathrm{CA}^{4-5}\mathrm{CO}^{4-5}\mathrm{S}^{4-5}}{\mathrm{P}(\underline{1:2})}$$

The gooseberries and currants constitute a rather clear-cut family of 1 genus and about 130 species. The family is closely related to the Saxifragaceae and by some authorities is included with them.

Familiar Examples.—Currants and gooseberries (*Ribes* spp.), both wild and cultivated, are the only examples of the family.

Stems and Roots.—The representatives of this family are all shrubs, rather small, mostly from 3 to 8 feet high, in thick clumps. Nearly all species of gooseberries are armed with spines that are extensions or protrusions of the cortex. The few strong spines at the nodes may be supplemented by weaker ones, "prickles," on the internodes.

Leaves.—The leaves are simple, serrate or dentate, and usually with about five lobes. They are alternate and generally long-petioled. Stipules are usually absent or, if present, are reduced to slight margins on the bases of the petioles.

Inflorescences and Flowers.—The typical inflorescence is an axillary raceme that is usually pendulous and sometimes reduced to three or fewer flowers. The flower is small, regular, and bisexual. It is epigynous, or nearly so, with the receptacle extending to form a "calyx tube" adherent to the ovary. This hypanthium, as it is called, continues in a circular ridge above the

attachment to the ovary, and to this the colored sepals, the tiny petals, and the stamens are attached. The sepals, petals, and stamens are five in number, or rarely four. The pistil is inferior and bicarpellate, with two styles, which are sometimes united, and two stigmas.

Fruits and Seeds.—The pistil with its adherent calyx tube grows into a very juicy berry, the wall of which is largely developed from the surrounding receptacle. It contains several seeds

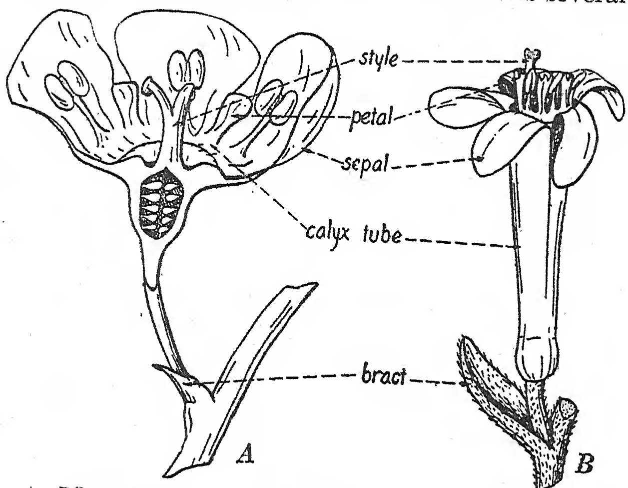


FIG. 61.—*A*, *Ribes rubrum*. *B*, *Ribes aureum* (Grossulariaceae). (*A*, *after Sargent; B, after Robbins.*)

and in some species is covered with minute spines. The embryo is small and straight with abundant endosperm.

Economic Significance.—Currants and gooseberries are well known for their richly flavored, strongly acid berries, which have become a staple product. Some of the wild species are edible, but others have a disagreeable flavor. Certain species are grown for their profuse yellow or red flowers and graceful form.

34. ONAGRACEAE. Eveningprimrose Family

$$\frac{\mathrm{CA}^4\mathrm{Co}^4\mathrm{S}^8}{\mathrm{P}④}$$

There are about 38 genera and 470 species, rather widely distributed, but most abundant in the subtropical portions of the Western Hemisphere

Familiar Examples.—Fuchsia (*Fuchsia* spp.), eveningprimrose (*Oenothera* spp.), and willowherb or fireweed (*Epilobium angustifolium* L.) are well-known examples of this family.

Stems and Roots.—The Onagraceae are nearly all annual herbs with a few biennials and occasional shrubby forms.

Leaves.—The leaves may be alternate or opposite and are simple and usually entire or nearly so, with stipules reduced to small glands or absent.

FIG. 62.—*Oenothera biennis* (Onagraceae). (*From Britton and Brown.*)

Inflorescences and Flowers.—The flowers are often very large, solitary, and axillary, or borne in racemes. They are bisexual, and mostly regular and 4-merous, although the number of sepals, petals, and stamens varies from two to nine. The sepals are borne on a tube that is adherent at its base to the ovary and often extends far above it. The distinct petals and sepals are inserted in the throat of the calyx tube. The pistil is composed of two to six carpels, generally four. Its ovary is inferior or nearly so, and the style is often very long to reach the length of the calyx tube.

Fruits and Seeds.—The fruit is generally a capsule containing many seeds, which are without endosperm and contain a straight or nearly straight embryo. In *Epilobium* the seeds bear a tuft of long silky hairs at one end, and these effectively aid in seed distribution.

Economic Significance.—As a rule the Onagraceae are unpalatable to livestock, but the fireweeds are an exception and are valuable forage plants where available. They are also important honey plants, and in burned-over areas they often spring up in great abundance. Many beautiful wild and cultivated plants belong to this family. These include the eveningprimroses, fuchsias, and Clarkias.

35. CUCURBITACEAE. Gourd Family

$$\frac{\mathrm{CA}^{\underset{\smile}{4-6}}\mathrm{Co}^{(\underline{4-6})}}{\mathrm{P}^{(\underline{1-3})}} \text{ or } \mathrm{CA}^{\underset{\smile}{4-6}}\mathrm{Co}^{(\underline{4-6})}\mathrm{S}^{1-5}$$

The Cucurbitaceae are essentially tropical and subtropical. It is hard for those who live in the northern United States to realize that there are about 100 genera and 800 species. Beyond the Canadian border only a few species can be grown out of doors at all.

Familiar Examples.—Familiar examples are pumpkin (*Cucurbita Pepo* L.), squash (*Cucurbita* spp.), cucumber (*Cucumis sativus* L.), muskmelon or cantaloup (*Cucumis Melo* L.), watermelon (*Citrullus vulgaris* Schrad.), and wild cucumber or balsam-apple (*Echinocystis lobata* (Michx.) T. and G.).

Stems and Roots.—The Cucurbitaceae are succulent, trailing or decumbent vines, usually climbing by means of tendrils. The stems of most species are hollow and five-angled with five corresponding bicollateral bundles.

Leaves.—The leaves are simple, but often deeply cleft, sometimes compound, usually exstipulate, large, and long-petioled. The petioles are often hollow. The arrangement on the stem is alternate. Concerning the morphology of the tendrils there is much difference of opinion. By some they are believed to be leaves, or that their branches are leaves and the main portion stem. By others they are considered bracteoles. It is almost certain that in *Kedrostis spinosa* they are stipules, and it may be that in different genera they are of different origin.

Inflorescences and Flowers.—The flowers are usually solitary in the axils, but in the small-flowered species they may be racemose or paniculate. They are unisexual and often dioecious. In structure the flowers are quite characteristic. They are 5-merous, but with the pistil tricarpellate by reduction, and the stamens united into two pairs, accompanied by a single one. The filaments are short, and the anthers long and slender but

Fig. 63.—*Cucurbita Pepo* (Cucurbitaceae). Staminate and pistillate flowers with portion of corolla removed to show pistils and stamens. (One-half natural size.)

folded or twisted into a compact mass. The style is short, surmounted by a broad three-lobed stigma.

Fruits and Seeds.—The fruit is a pepo or gourd, rarely a capsule, often of huge size; indeed, the largest of all fruits are found in this family. The seeds are numerous, generally large and flat, and with no endosperm. The embryo is straight, with large, oily cotyledons.

Economic Significance.—The Cucurbitaceae have long played an important part in the affairs of mankind. Gourds of various shapes and sizes have been extensively used as primitive vessels

and utensils. The food value, delicious flavor, and abundant production of the fruits have given them a prominent place. In addition to the familiar pumpkins, squashes, and melons, numerous other kinds are found in the tropics. To some extent, wild cucumber and other vines are grown on trellises for ornamental purposes.

36. CACTACEAE. Cactus Family

$$\frac{\mathrm{Ca}\,\infty\ \mathrm{Co}\,\infty\ \mathrm{S}\,\infty}{\mathrm{P}\left(\underline{1:3\text{–}\infty}\right)}$$

About 100 genera and 1,000 species, restricted almost exclusively to North and South America and most numerous in Mexico and Central America. Only one genus, *Rhipsalis*, is native to the Eastern Hemisphere. This is composed of epiphytes and is found in the tropics of Asia and Africa. The cacti are typically xerophytic and tropical but extend through the semiarid region of the west into southern Canada.

Familiar Examples.—Few cacti grow wild in the United States except in the far west, where the pricklypear (*Opuntia* spp.) is a common desert plant, and in the extreme southwest where many species are abundant. Nightblooming-cereus (*Hylocereus undatus* Britt. and Rose) is often grown in dooryards, and crab-cactus (*Zygocactus truncatus* Schum.), rattail cactus (*Aporocactus flagelliformis* Lem.), and many other species are commonly found in greenhouses and conservatories.

Stems and Roots.—Cactus stems are peculiar in appearance. They are thick and fleshy, and while some grow 50 to 60 feet high they can hardly be called shrubs or trees because of their texture. They are subglobose to cylindrical or flattened and most of them have prominent vertical ridges. Almost invariably they are spiny, sometimes extremely so, the spines growing from rounded cushions or tubercles composed of a combination of leaf base and rudimentary branch. In many cases at least, the larger spines, and perhaps all, should be looked upon as specialized leaf parts. The root system is small and shallow for xerophytic plants of their size.

Leaves.—Cacti are commonly described as leafless, the leaves being reduced to spines as stated above. In *Opuntia* a few small awl-shaped leaves develop and fall when very young. The func-

tion of photosynthesis is assumed by the dark-green stems. Two tropical genera show a mesophytic structure, with slender branches and broad simple leaves.

Inflorescences and Flowers.—The flowers are solitary, large, and showy. Generally they are regular or nearly so, but in some species the sepals are petaloid, or the petals sepaloid,

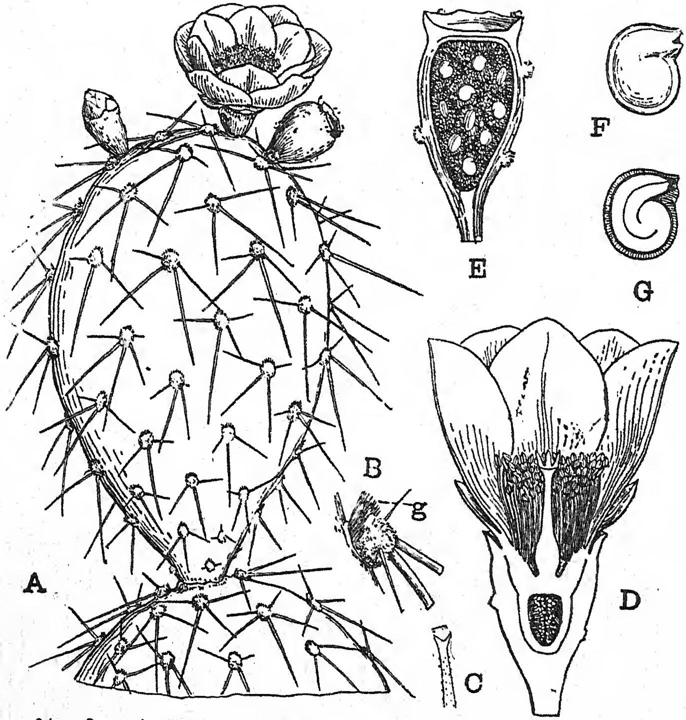


FIG. 64.—*Opuntia Tuna* (Cactaceae). *A*, portion of stem with bud, flower, and fruit. *B*, cluster of spines. *C*, single bristle. *D*, longitudinal section of flower. *E*, longitudinal section of fruit. *F*, seed (external). *G*, seed (internal). (*After Rendle.*)

making the two intergrading or indistinguishable. Perianth segments and stamens are generally numerous with epigynous insertion on the inferior ovary. The pistil is composed of several closely united carpels with one seed chamber.

Fruits and Seeds.—The fruit is a rather compact, many-seeded berry. The seeds contain endosperm in varying amounts. The embryo varies from straight to semicircular.

Economic Significance.—The Cactaceae are of especial scientific interest because of their extreme adaptation to xerophytic conditions. They also have considerable economic importance. Their peculiar forms and gorgeous flowers have been given some recognition in the greenhouse, and the traveler in the American tropics is impressed with their adaptability to their environment. The use of cacti for rock gardens and planting under unusual conditions has become quite extensive, and societies have been formed for their study and promotion. In Mexico cacti are sometimes grown for hedges. The fruits of some species are sweet and of good flavor, but their use is rather local. That the stems of some are nutritious is well established, but their compact form, vicious spines, and sometimes disagreeable taste have given them general immunity from consumption by livestock. Even that recent introduction, the spineless cactus, is but a partial success.

37. VITACEAE. Grape Family

$$\mathrm{Ca}^{4-5}\mathrm{Co}^{4-5}\mathrm{S}^{4-5}\mathrm{P}②$$

The grape family contains only about 10 genera and 500 species. They are widely distributed in temperate and subtropical regions.

Familiar Examples.—Grape (*Vitis* spp.), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.), and Boston ivy (*P. tricuspidata* Planch.) are well-known examples of this family.

Stems and Roots.—The Vitaceae are mostly vines, climbing by tendrils or by adventitious roots. The tendrils have a special morphological interest. They are borne at the nodes, opposite the leaves, and it is held on good authority that each represents the tip of the main shoot that has been pushed aside by the growth of a lateral bud at its base. In some species the tendrils develop adhesive disks at their tips. A few tropical species are shrubs or small trees. The nodes are enlarged and the vines and tendrils are tough and strong. The grape, especially, contains an abundance of watery juice.

Leaves.—The leaves may be simple as in the grape, or they may be compound as in the Virginia creeper. They are petiolate with deciduous stipules and an alternate arrangement.

Inflorescences and Flowers.—The flowers are usually borne in panicles or cymes, which take the place of tendrils opposite the

leaves at certain nodes. They are small and either bisexual or unisexual, in some species dioecious. The calyx is four or five toothed or reduced to an inconspicuous ring. The petals are of the same number, greenish in color, and generally fall as soon as the flower opens. There are four or five stamens, always opposite the petals, and a bicarpellate pistil, which is more or less embedded in a circular disk.

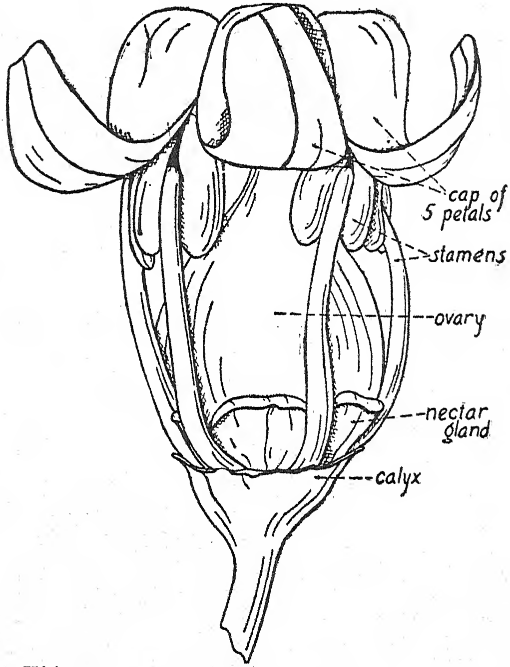


FIG. 65.—*Vitis* (Vitaceae). Partly opened flower. (*After Robbins.*)

Fruits and Seeds.—The fruit is a berry, well illustrated by the grape. The seed contains oily endosperm and a small embryo.

Economic Significance.—Grapes are extensively raised the world over in all but the colder climates. Their use for food and for wine goes back to the dawn of civilization, and much attention has been given to the development of varieties especially suited to the different uses. Vast quantities are dried into raisins, and the so-called dried currants are in reality made from certain varieties of tiny grapes.

In the east, middle west, and south the Vitaceae furnish the

best of our climbing woody vines, some species having the very desirable feature of clinging to brick or stone buildings by short tendrils with disk-like ends or by aerial roots, thus eliminating the need of trellises. They are made more attractive by their brilliant autumn colorings.

38. LORANTHACEAE. Mistletoe Family

$$\frac{\mathrm{Ca}^{2-3}\,\dfrac{\mathrm{S}^{3-0}}{\mathrm{Co}^{2-3}}}{\mathrm{P}(\underline{1:2})\text{–}0}$$

The mistletoe family consists of about 21 genera and 500 species, mostly tropical and subtropical, but a few found in temperate climates. Nearly all are parasitic on trees and shrubs. Only two genera and nine species are found in the United States and the following account is restricted to them.

Familiar Examples.—American-mistletoe (*Phorandendron* spp.) and small or lesser mistletoe (*Arceuthobium* spp.) are the best known examples of this family.

Stems and Roots.—Our mistletoes are small, perennial, usually shrubby plants that grow as parasites on various trees. In length they vary from 1 to 8 inches. The branching is dichotomous. The root takes the form of a haustorium that penetrates the bark and sapwood of the host and from this source obtains a part or all of the nourishment required by the plant. *Phoradendron* attacks chiefly angiosperms, such as poplars, willows, oaks, and acacia, while *Arceuthobium* attacks gymnosperms, such as pine, larch, and Douglasfir.

Leaves.—The mistletoes are evergreen, and the larger forms are sometimes so abundant in a tree that they give it a leafy appearance during the winter. The leaves are opposite and entire, without stipules. In *Phoradendron* they are about 1 inch long and half as broad, with a pale-green color. They are therefore able to contribute something to the nourishment of the plant. In *Arceuthobium* they are reduced to functionless scales, and the plant is strictly parasitic.

Inflorescences and Flowers.—The flowers are solitary or few in the axils of the leaves. They are unisexual and dioecious, regular, and apetalous, with an inferior ovary.

Fruits and Seeds.—The fruit is commonly called a berry, but it is morphologically a tiny one- to three-seeded pome, the fleshy

receptacle covering the ovary. This outer covering becomes viscid, enabling it to adhere to the beaks of the birds that have attempted to eat the fruits and to the feet of birds and squirrels that happen to have run over them. They are thus carried to other branches where they adhere with sufficient strength to enable the germinating seed to penetrate the bark. The seeds contain endosperm and the embryo is straight.

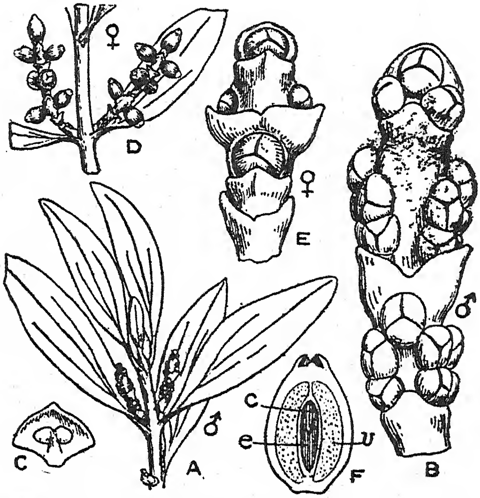


Fig. 66.—*Phoradendron Wattii* (Loranthaceae). *A*, staminate spikes. *B*, single staminate spike. *C*, petal with stamen. *D*, pistillate spikes. *E*, single pistillate spike. *F*, longitudinal section of fruit. (*After Rendle.*)

Economic Significance.—The Loranthaceae are of no value except as objects of curiosity, and of sentiment in the case of the English mistletoe. They do some damage by distorting their hosts at the point of attachment.

39. ACERACEAE. Maple Family

$$\mathrm{Ca}^{5(4-12)}\mathrm{Co}^{0-5(-12)}\mathrm{S}^{0-12}\mathrm{P}^{0-②}$$

The maple family is a small one, containing only 2 genera and about 100 species. They are mostly confined to the North Temperate Zone and are especially prevalent in the eastern half of the United States. Like so many of our trees, their ancestry can be traced back to the Cretaceous period. Their place of origin appears to have been northen Canada or Greenland. The Glacial epoch greatly reduced the area covered by the maples and nearly

exterminated them from northern and central Europe, but most species survived in favored localities. As a result we often find the same species in restricted spots on both continents of the Northern Hemisphere, with thousands of miles intervening. Occasionally they make nearly solid forests, but more often they are mixed with trees of other families.

Familiar Examples.—The maples (*Acer* spp.) and the box-elder (*A. Negundo* L.) are examples of this family.

Stems and Roots.—Nearly all members of the family are trees, some of them more than 100 feet high and 3 to 4 feet in diameter. A few species are shrubs. In forests the trunks of most species are straight, with the lower half free from branches. Standing alone, the trees branch widely and are nearly as broad as high. They are rather slow in growing but long-lived. The buds are prominent and protected by large scales.

Leaves.—The leaves are broad, variously cleft, or, in the box-elder, pinnately compound. They are petiolate, exstipulate, and opposite.

Inflorescences and Flowers.—The flowers are borne in small axillary clusters, which take the form of racemes or cymes. They may be either bisexual or unisexual. Most maples are polygamous, the same inflorescence bearing both bisexual and unisexual flowers. The box elder is dioecious. In bisexual flowers there are generally five distinct sepals, five small, distinct, regular petals, eight stamens, and one bicarpellate pistil with two styles and a superior ovary.

Fruits and Seeds.—The fruit is a characteristic samara with one wing, each flower producing a pair, loosely attached to each other at the base, with wings diverging. These are the well-known "keys." The embryo is curved or crumpled, and there is usually no endosperm.

Economic Significance.—The maples are among our most valuable forest trees. The lumber is cut to the extent of a billion board feet annually in the United States. It is exceedingly hard, strong, and close-grained, and some varieties or individuals develop the beautiful bird's-eye grain so much prized for furniture and musical instruments. With the exception of oak no other wood is used so much for implements and hardwood floors. For fuel it is famous, and the maple backlog for the fireplace has become celebrated throughout the east. The fertilizer value of

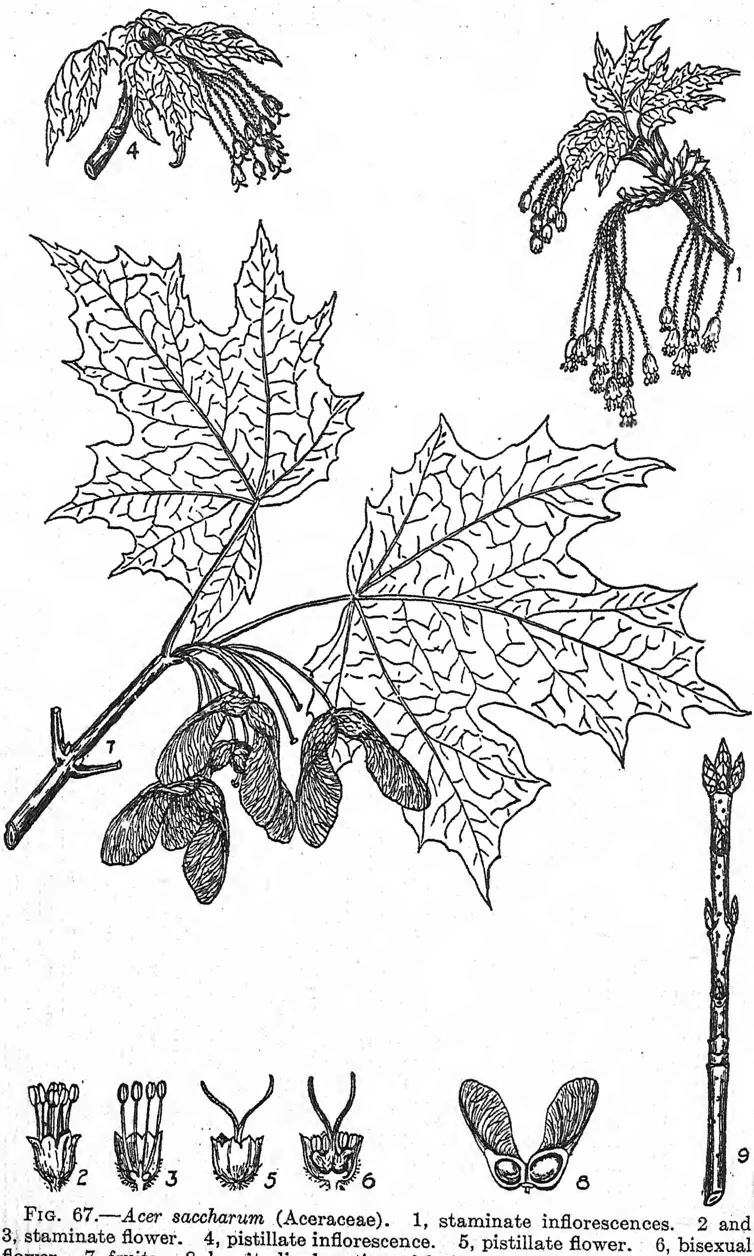


FIG. 67.—*Acer saccharum* (Aceraceae). 1, staminate inflorescences. 2 and 3, staminate flower. 4, pistillate inflorescence. 5, pistillate flower. 6, bisexual flower. 7, fruits. 8, longitudinal section of fruits. 9, twig with leaf scars and buds. (*After Illick.*)

the leaves and the ashes has long been recognized. For ornamental planting the maple trees will hold their own with the best. Nor must we forget the delicious maple sugar and syrup obtained from the sap of *Acer saccharum* Marsh. The maple family is one having many good traits and no bad ones.

40. ANACARDIACEAE. Cashew Family

$$\mathrm{Ca}^{3-7}\mathrm{Co}^{3-7}\mathrm{S}^{3-\infty}\mathrm{P}^{1-5}$$

This family has a wide distribution in temperate and tropical regions. There are about 65 genera and 500 species.

Familiar Examples.—The best known examples growing in the United States are the sumacs (*Rhus* spp.) and several poisonous species of *Rhus* variously known as poisonivy, poisonoak, poisonsumac, and poisonelder. Imported from the tropics are pistachio nuts (*Pistachia vera* L.) and cashew nuts (*Anacardium occidentale* L.).

Stems and Roots.—This is a family of trees, shrubs, and woody vines with resinous bark.

Leaves.—The leaves are generally alternate and either simple or compound. A few species are evergreen.

Inflorescences and Flowers.—Most species bear their flowers in panicles. These flowers are usually small, bisexual, and irregular, having three to seven petals—commonly five—with stamens of the same number or twice as many. The number of carpels varies from one to five. The receptacle is conspicuously broad and fleshy.

Fruits and Seeds.—The fruit of most Anacardiaceae is a drupe, but in some it is a few-seeded berry.

Economic Significance.—The proportion of species of this family that is of significance to man is relatively large. The fruits or seeds of a considerable number are highly prized for food. These include the pistachio and cashew nuts and the mango. Because of their shapeliness and colored foliage and fruits, many are extensively grown as ornamentals. A few, including poisonivy, are skin irritants.

41. JUGLANDACEAE. Walnut Family

$$\mathrm{Ca}^{3-9}\mathrm{Co}^{0}\mathrm{S}^{3-\infty} \text{ or } \frac{\mathrm{Ca}^{0}\mathrm{Co}^{0}}{\mathrm{P}(1:2)}$$

In the Juglandaceae we have a small family of fine large trees. There are but 6 genera and 35 species. In all likelihood they are

not genetically close to the other Amentiferae, *e.g.*, the birches and the poplars.

Apparently the Juglandaceae were once more abundant than now. Their remains are found in Cretaceous rocks, and throughout the most of the Cenozoic era they were widely distributed over the Northern Hemisphere, with the exception of the arctic regions. The frigid climate that generally prevailed in the North Temperate Zone during the Pleistocene epoch exterminated them except in favored localities. Europe lost all of her hickories and nearly all of her walnuts, the survivors being restricted to the eastern Mediterranean region.

Familiar Examples.—Well-known examples of the Juglandaceae are walnuts (*Juglans nigra* L. and *J. regia* L.), butternut (*J. cinerea* L.), hickories (*Carya* spp.), and pecan (*Carya Pecan* Aschers. and Graebn.).

Stems and Roots.—The existing members of the Juglandaceae are all trees, often of considerable size. The pecan and the black walnut grow to a height of 150 feet and a diameter of 6 feet. When somewhat crowded, they have straight, smooth trunks, the lower half free from branches. Standing alone, they are widely branching and of striking appearance. The young bark is glandular and somewhat aromatic, and the pith in walnut and butternut is diaphragmed, *i.e.*, filled with thin, hard, horizontal partitions set at close intervals, in longitudinal section appearing like a ladder.

In most species two or three buds may be found above each leaf. The lowest is in the axil of the leaf, or slightly above, and the others are superposed in a row, with small intervals between. The buds are large and well protected by stout scales, which are often densely pubescent. The leaf scars are very large and conspicuous.

Leaves.—The leaves are odd-pinnately compound and very large in some species. In black walnut and butternut, which commonly have thirteen to nineteen leaflets, they are as much as 2 feet long and very handsome. The leaflets vary from lanceolate to ovate, with finely serrate margins, and have a viscid aromatic pubescence, especially on the lower surface. The arrangement on the stem is alternate.

Inflorescences and Flowers.—The flowers in the Juglandaceae are unisexual, the staminate in pendulous aments, and the

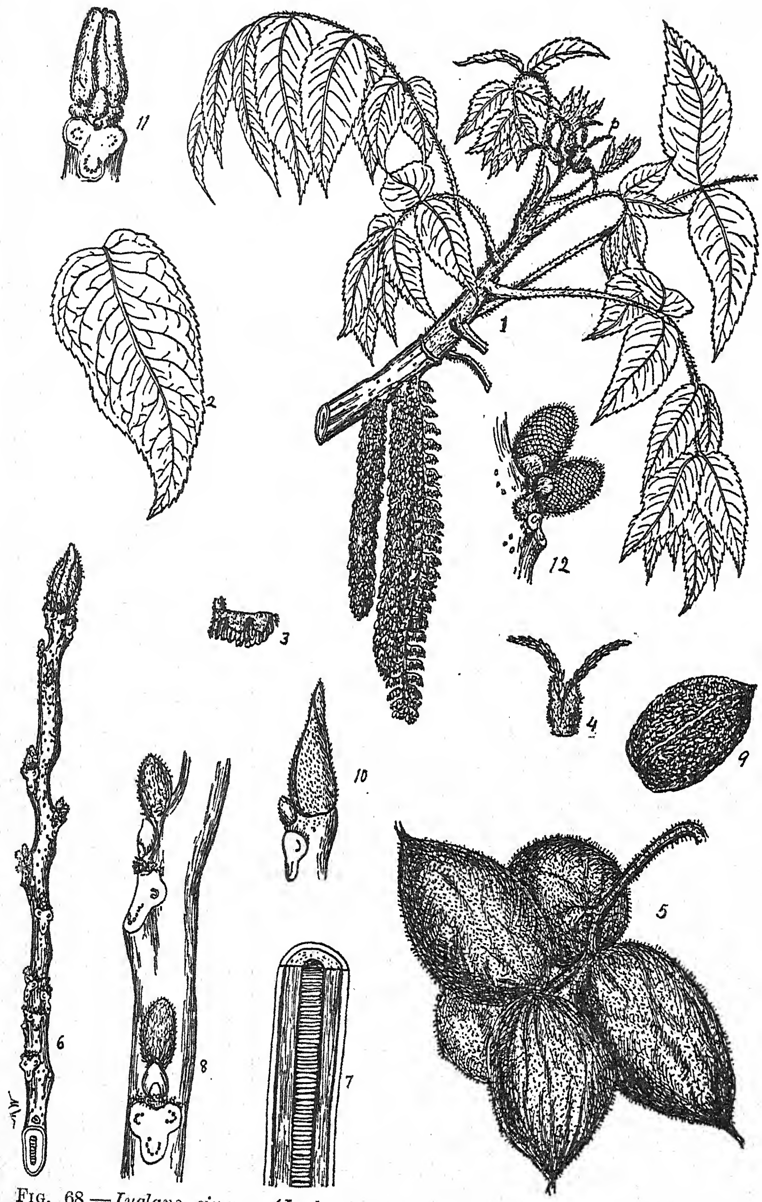


FIG. 68.—*Juglans cinerea* (Juglandaceae). 1, branch with staminate and pistillate flowers. 2, leaflet. 3, staminate flower. 4, pistillate flower. 5, fruits. 6, twig. 7, longitudinal section of twig. 8, leaf scar and superposed buds. 9, nut with husk removed. 10 and 11, terminal buds. 12, lateral buds. (*After Illick.*)

pistillate solitary or few in a group. Both kinds are borne on the same tree.

The staminate aments are borne just above the leaf scars of the previous season. They may be either single or in clusters of two or three, and are from 3 to 5 inches long. Each ament produces many staminate flowers. Each flower consists of a group of several pollen sacs, surrounded in most cases by a two- to six-lobed perianth. This flower is set in the axil of a bract with a small bracteole on either side. Occasionally a rudimentary pistil is borne in the staminate flower.

The pistillate flowers are borne at the tips of the twigs. Each consists of a bicarpellate pistil with a calyx of four lobes (sometimes three or five), and often with as many tiny petals. The ovary is inferior, or nearly so, with one ovule and two stigmatic styles. The pistillate flower, like the staminate, is set in the axil of a bract with two lateral bracteoles. It is not ready for fertilization until after the pollen is shed.

It will be noted that such flowers are far from primitive but show a considerable degree of specialization.

Fruits and Seeds.—The fruit is a nut, or, in reality, a sort of dry drupe. The thick outer wall or husk is tough and leathery and in some species dehiscent. It appears to be formed by a fusion of bract, bracteoles, and perianth. The inner shell or pericarp is exceedingly hard. It consists of the matured ovary wall. The nut contains a single seed with two large, lobed, and convolute cotyledons and no endosperm.

In certain genera, no longer found in the United States, notably *Engelhardtia*, the fruit is small, with large wings, a samara.

Economic Significance.—In proportion to the number of individuals the Juglandaceae are of great importance. The fruits of the walnut, butternut, pecan, and some species of hickory are very highly prized and grown in considerable abundance. The wood of black walnut is so desirable for furniture, interior finishing, etc., that it has been cut almost to extermination. It is rather dark, even-grained, strong, easy to work, and holds its shape well. The wood of the butternut is softer and weaker and yet of fair quality. In hickory we have one of the greatest of all woods for certain purposes. It is light in color, very close- and even-grained, and exceedingly strong, especially the second growth that has sprouted up from stumps and grown into small

trees. No other wood can replace it where extreme toughness is required, as for hammer and axe handles, and spokes, shafts, tongues, and other parts of wagons. The wood of the pecan is intermediate in weight and strength between walnut and hickory. Unfortunately, the trees of this family have a very limited range. They are more abundant in the United States than elsewhere, but here they are found only irregularly in the eastern and southeastern sections and on the Pacific coast. The demand has greatly exceeded the supply with the results that one would expect.

Aside from their value for lumber and nuts, the walnut and butternut are highly desirable for ornamental trees, since their great spreading tops and magnificent foliage are hardly surpassed by any other trees.

42. FAGACEAE. Beech or Oak Family

$$\mathrm{Ca}^{\underset{\smile}{4-7}}\mathrm{Co}^{0}\mathrm{S}^{3-\infty} \text{ or } \frac{\mathrm{Ca}^{\underset{\smile}{4-7}}\mathrm{Co}^{0}}{\mathrm{P}^{(\underline{3-7})}}$$

Members of the Fagaceae are familiar to nearly all who live in the vicinity of deciduous forests. There are 6 genera and about 350 species. They are earliest known from the Cretaceous rocks, and during most of the Cenozoic era they were abundant and cosmopolitan. While the Glacial epoch reduced them considerably, they are still numerous throughout the North Temperate Zone with some extensions into the South Temperate.

Familiar Examples.—Familiar examples of the Fagaceae are beech (*Fagus grandifolia* Ehr.), oak (*Quercus* spp.), and chestnut (*Castanea* spp.), but not the horsechestnut (*Aesculus* spp.), which belongs to another family (Sapindaceae).

Stems and Roots.—All of the family are either trees or shrubs. In each of the three more important genera trees can be found more than 100 feet high and 6 feet in diameter, and a few old monarchs greatly exceed this size. Where grown thickly in the forest the trees have straight, smooth, branchless trunks for half to three-fourths of their height. Growing solitary in the open they form magnificent spreading tops, the lowest branches being but a few feet from the ground.

The roots are somewhat variable. In the beech the older ones near the great trunks are exposed above the surface of the ground. The oaks are very deep-rooted forming almost a taproot in

some cases. The chestnuts are intermediate in depth of root system.

Leaves.—The leaves are alternate, simple, petiolate, entire in a few species, but generally toothed or cleft. Where stipules form, they are fugacious. In *Castanea* and usually in *Fagus* the leaves are deciduous. In *Castanopsis* and *Lithocarpus* they are evergreen, while in *Quercus* both kinds are found in different species.

Inflorescences and Flowers.—All species are monoecious with unisexual apetalous flowers. In *Fagus* the staminate flowers are in dense umbel-like clusters. In the other genera they are in aments, erect or pendulous, often large and abundant, giving the tree a beautiful appearance when in bloom. The pistillate flowers are solitary or two or three in a cluster.

The staminate flowers are borne in deciduous bracts and consist of a small cluster of stamens in a cup-shaped, four- to seven-toothed calyx. A rudimentary pistil is sometimes found with the stamens. The pistillate flowers are three- to seven-carpellate with as many chambers and styles as carpels. There are one or two ovules in each chamber, but only one in each ovary develops. The ovary is enclosed in a perigynous four- to eight-toothed calyx that occasionally includes rudimentary stamens also. A many-scaled involucre surrounds the base of each flower.

Fruits and Seeds.—In most species the fruit matures the first season, but in *Castanopsis*, *Lithocarpus*, and some species of *Quercus* not until the end of the second season. The fruit is a nut, borne singly or in twos or threes, in a dense involucre. In the oaks the involucre forms a rough basal cup. In beech, chestnut, and chinkapin it is a prickly bur entirely covering the fruit and opening by four valves at maturity. In the beech and chinkapin the nuts are angled. In the oak and chestnut they are rounded except that in the latter the compressed surfaces of the adjoining three are somewhat flattened. The seed is without endosperm, starchy, nutritious, and well flavored except in the oaks, where in most species it is bitter.

Economic Significance.—The family Fagaceae is the most important of the woody angiosperms. The great abundance and high quality of the wood are well known. Probably more high-class furniture is made from oak than from all other kinds of lumber combined. It is extensively used for floors and interior work. In the days of wooden vessels it was the mainstay in ship-

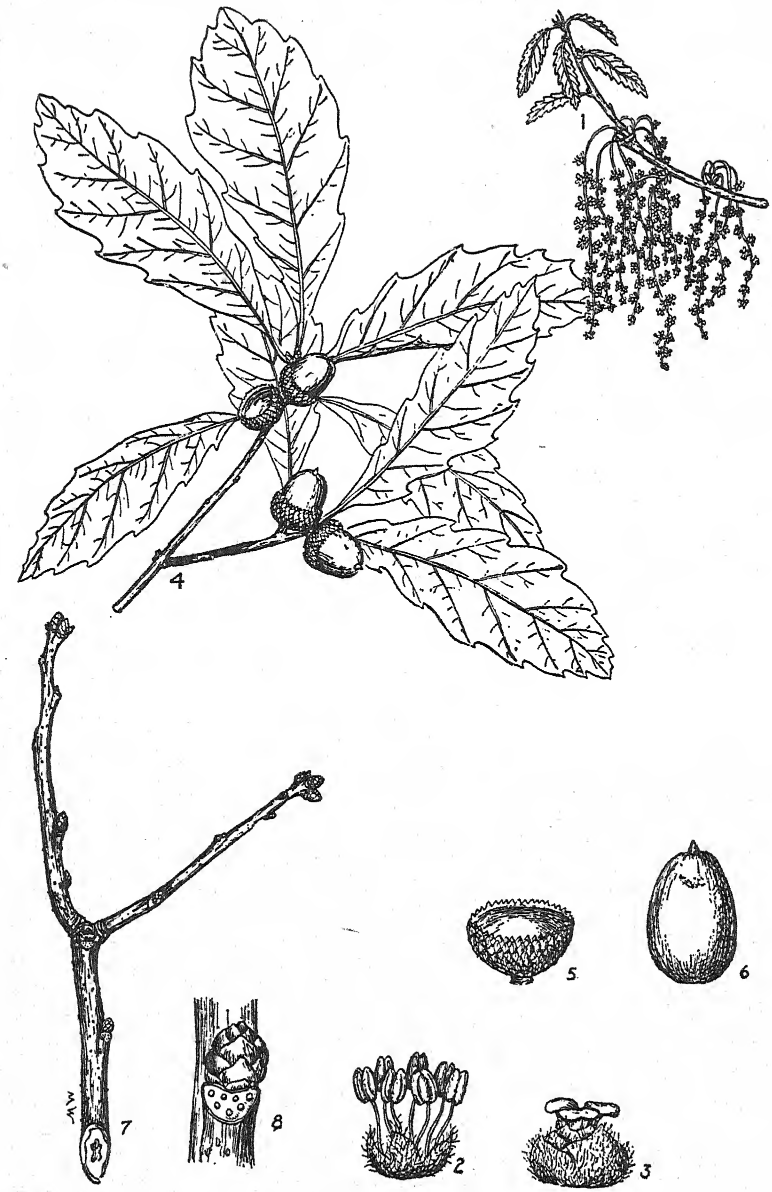


Fig. 69.—*Quercus prinoides* (Fagaceae) 1, branch with staminate aments. 2, staminate flower. 3, pistillate flower. 4, fruiting branch. 5, acorn cup formed from the involucre. 6, fruit (acorn). 7, twig in winter condition. 8, leaf scar and lateral buds. (*After Illick.*)

building. Its sturdiness is a tradition the world over. The wood of beech is as heavy and strong as that of most of the oaks, much more even-grained, and almost impossible to split. It is very resistant to the action of water and free from objectionable taste, hence its extensive use for household utensils, spoons, plates, tubs, vats, etc. Its use in shipbuilding has been second only to that of oak. Chestnut yields a lighter wood not well suited to building purposes where exposed to the weather, on account of checking and warping, but of great value for fence posts, mine props, telephone and telegraph poles, and railroad ties. The devastation caused by the chestnut blight has been one of the greatest tragedies of the eastern forests.

All members of the family are excellent for fuel and are extensively used for this purpose. The oak and beech are rather slow-growing, but the chestnut grows rapidly, especially the second growth sprouting up from stumps.

Throughout all the history of Europe the beech and oak have played a conspicuous part in the traditions, sentiment, and superstitions of the people. The oak has long been symbolic of protective strength. In all regions where these trees will grow they rank among the first for ornamental planting.

The oaks, especially, show a marked tendency to produce cork in the bark. This development reaches its climax in the cork oak (*Quercus Suber* L.), from which it is removed in great sheets for technical use. The bark of other oaks is extensively used in tanning leather.

The nuts of beech, chinkapin, and chestnut are of the finest quality, and a few species of oak, especially *Quercus Michauxii* Nutt., produce edible acorns. Few species of nuts are produced in such quantities as the chestnut. In crowded forests the yield is low, but where the trees are scattered they bear heavily. This nut is so abundant and so desirable as a food product that in some parts of Europe it is even dried and ground into flour. Certain Asiatic and cultivated varieties are much larger than the American species but inferior in flavor.

Where beechnuts, chestnuts, and acorns are abundant, they are a valuable source of feed for swine; these animals eat the fruit of all species regardless of bitter flavors, and they can find them among fallen leaves where human beings would have little success.

43. BETULACEAE. Birch Family

$$\text{Ca}^{4-0}\text{Co}^{0}\text{S}^{2-10} \text{ or } \frac{\text{Ca}^{0}\text{Co}^{0}}{\text{P}②}$$

The birches and their relatives are well known throughout the deciduous-forest regions of the country. There are 6 genera and about 80 species found mostly in the North Temperate Zone but a few extending into the South Temperate Zone in the Andean region. The arctic birches of today are found as far north as any woody plants, but in the latitude of northern United States and central Europe they are at their best. Their earliest remains are from Cretaceous rocks, and throughout most of the Cenozoic era a considerable number of species flourished that are now extinct. On the whole, however, they held their own through the Glacial epoch better than did most plants.

Familiar Examples.—The best known of the Betulaceae are birches (*Betula* spp.), alders (*Alnus* spp.), and hazelnut and filbert (*Corylus* spp.).

Stems and Roots.—The Betulaceae are all woody, varying in size from the dwarf arctic birches to the yellow, black, and canoe birches, which are sometimes more than 100 feet high and 4 feet in diameter. One of the conspicuous characters of the family is the periderm, the thin corky outside layer of the bark that in the birches especially can be peeled off like a sheet of paper. The color varies from very dark brown through red-brown and yellow to almost snow-white. The young shoots are slender, elastic, and tough, so much so that the quality of the birch rod of the schoolroom has become traditional. Terminal leaf buds are not formed at the close of the growing season (except in *Alnus*), and the shoot continues its growth the next year through the activity of a lateral bud near the tip.

Leaves.—The leaves are simple, serrate, and petiolate, with an alternate arrangement on the stem. In the unfolding bud they have stipules, but these fall off as the leaves expand.

Inflorescences and Flowers.—The flowers are unisexual and usually monoecious. Both kinds are borne in aments that are well begun the season before flowering and rest over winter unprotected by bud scales. Sometimes two or more grow from the same node.

The staminate aments, when expanded, are 1½ to 4 inches

FIG. 70.—*Betula papyrifera* (Betulaceae). 1, branch with staminate and pistillate flowers. 2, same, but more advanced stage. 3, fruit. 4, scale of strobilus. 5, staminate ament. 6 and 7, lateral buds and leaf scars. (*After Illick.*)

long and pendulous. In the axil of each scale are one to three flowers, three apparently being the typical number, which is reduced in some species. There may or may not be a calyx. If present, it consists of a four-, five-, or six-toothed shallow cup. Petals are absent. The flowers adhere to the bracts and there may be two or four bracteoles more or less united with each bract at its margins.

The pistillate aments are shorter than the staminate (generally a fraction of an inch), erect when young, but somewhat pendulous at maturity. In *Corylus* they are reduced to a few flowers. Two or three flowers are borne in the axil of each scale. The calyx, if present, adheres to the ovary, making the latter inferior. The pistil is bicarpellate, with one or two styles and two stigmas. One or two ovules are found in each chamber of the ovary. In most species the ovules are immature at the time of pollination, and the pollen grains germinate and penetrate the styles where they lie dormant for several weeks, until the ovules are ready for fertilization.

Fruits and Seeds.—In most of the Betulaceae the pistillate aments develop into woody cones, doubtfully homologous with the strobili of the gymnosperms. In these matured inflorescences are found seed-like fruits (nutlets), generally one to each scale. In many species they are winged—either two lateral wings or a circular one.

In the hazelnut (*Corylus*) the fruits are larger, ½ to ¾ inch in diameter, nearly spherical, wingless, and borne in pairs. Each nut is covered by a husk that grows over it from the base and extends an inch or so beyond the apex in the form of a tube. This husk consists of an involucre made up of two united bractlets. The surface is thickly set with stiff, sharp, protective hairs.

Each fruit contains one seed with relatively large cotyledons and no endosperm. The embryo is straight.

Economic Significance.—Few families of woody dicotyledons are as important in northern and temperate countries as the Betulaceae. The wood of the larger birches is of high quality, hard, heavy, strong, and even-grained. It is somewhat similar to that of some of the maples. When seasoned it holds its shape well and is used very extensively for interior finishing, floors, furniture, and various small articles such as Indian clubs and

other athletic goods, spools, and baskets. When suitably stained it makes an excellent imitation of mahogany. For fuel birch is hardly surpassed by any wood, and alder has been extensively used in the manufacture of charcoal and of black gunpowder.

The bark of several species has been very widely used in basketry, but the great utility of birch bark is for canoes. These light, responsive crafts have for centuries been the chief means of navigation on the swift streams of northern United States and Canada. Extensively used by the Indians, who made them with remarkable skill, they made possible much of the exploration of the American continent by the early traders and missionaries. Thousands of them are still in use, notwithstanding the competition of the canvas canoes made in imitation of them. The tree generally used in their manufacture is the canoe birch (*Betula papyrifera* Marsh.), the white tough bark of which can be peeled off in large sheets.

The inner bark of the birches is rich in starch and in some species, *e.g.*, sweet or black birch (*Betula lenta* L.), it is very palatable and has been extensively eaten in times of distress. There is no better browse for livestock, deer, etc., than birch twigs, either with or without leaves. Hazelnuts and filberts, both being sold under the latter name, are among the best nuts we have. A good, inexpensive imitation of oil of wintergreen is extracted from the bark.

The birch has been well named "The Lady of the Woods." Few, if any, trees surpass it in grace and beauty. The white species, especially, are extensively grown on public and private grounds and reach their supreme development in the cut-leaved weeping birch, a horticultural variety of *Betula alba* L.

44. CORNACEAE. Dogwood Family

$$\frac{\mathrm{C}\textsc{a}^{4-5}\mathrm{Co}^{4-5}\mathrm{S}^{4-5}}{\mathrm{P}(\overline{\underline{1-4}})}.$$

Of the Cornaceae there are 10 genera but only about 115 species. These are found mostly in the North Temperate Zone, with a little extension into South America. There are indications that they originated in what is now northern Canada or Greenland and spread to all the continents of the Northern Hemisphere. Their lineage dates back to the Cretaceous period, but they have never been a conspicuous part of the earth's flora. At present they

are found scattered through forests of other trees and along the banks of streams over a wide area.

Familiar Examples.—Flowering dogwood (*Cornus florida* L.), Pacific dogwood (*Cornus Nuttallii* Aud.), the common small-flowered dogwood (*Cornus* spp.), blackgum (*Nyssa sylvatica* Marsh), and tupelo (*Nyssa* spp.) are representative examples.

Stems and Roots.—The Cornaceae are mostly shrubs, but the Pacific dogwood is a tree, sometimes 60 feet high and 1 foot in diameter. Several species are conspicuous for the color of their bark, which is green in some but deep red in others. The wood of the eastern flowering dogwood is exceedingly hard and close grained. The pepperidge or sour-gum trees tend to become hollow as they grow older and are often inhabited by wild bees, hence the use of the term "gum" as a colloquial name for a beehive.

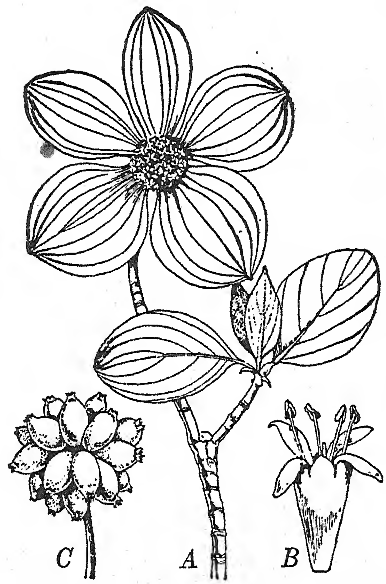


FIG. 71.—*Cornus Nuttallii* (Cornaceae). *A*, flower cluster encircled by petal-like bracts. *B*, single flower. *C*, cluster of fruits. (*After Jepson*).

Leaves.—The leaves are simple and usually entire, petiolate, and exstipulate. Their arrangement is generally opposite.

Inflorescences and Flowers. The inflorescence is usually a cyme or a panicle, but it may be a head with four to six large petaloid bracts at the base. The flowers are small, regular, and mostly bisexual and 4-merous, except for the bicarpellate ovary. The insertion is epigynous. In the so-called flowering dogwood, the inflorescence is practically a head of tiny flowers inside of a whorl of four, five, or six large, white or pink, showy bracts, which are commonly mistaken for petals. The whole effect is that of a single flower 3 to 4 inches in diameter.

Fruits and Seeds.—The fruit is a small berry-like drupelet which at maturity may be red, white, blue, or green. It contains

one or two seeds with copious endosperm. The embryo is often small.

Economic Significance.—In two respects the Cornaceae are valuable. The dogwoods are ornamental shrubs, some prized for their bright-red bark, which gives them a striking appearance through the winter when the leaves are gone, and some for the large, showy, petal-like flower bracts. These "false flowers," as they may be called, appear in the undergrowth of the forest early in the season and are of striking beauty, some of them being 3 inches or more in diameter. The tupelo trees of southeastern United States yield a great abundance of nectar that makes honey of a high quality.

45. UMBELLIFERAE (AMMIACEAE). Carrot Family

$$\frac{\mathrm{CA}^5\mathrm{Co}^5\mathrm{S}^5}{\mathrm{P}②}$$

The family Umbelliferae is a rather large one, containing about 270 genera and 2,700 species. They are widely distributed but most abundant in the North Temperate Zone.

Familiar Examples.—Familiar examples are carrot (*Daucus Carota* var. *sativa* DC.), parsnip (*Pastinaca sativa* L.), parsley (*Petroselinum hortense* Hoffm.), and celery (*Apium graveolens* L.).

Stems and Roots.—The Umbelliferae are herbaceous, with a predominance of perennials, although biennials and annuals are numerous also. In many species the nodes are conspicuously enlarged and the internodes are hollow. Commonly the stems are vertically ridged. The roots are large—tap, fascicled, or irregular—and often fleshy. Rootstocks are found in some species.

Leaves.—With few exceptions the leaves are pinnately compound and often decompound. The petiole is often swollen, even hollow at the base, and sheathing the stem. Stipules are rare, and when present they are small or membranous. The arrangement is alternate.

Inflorescences and Flowers.—As would be expected from the name of the family, the inflorescence is usually an umbel. It is reduced to a single flower in some species of *Azorella* and *Hydrocotyle*, however, and forms a compact head in *Eryngium*. The flowers are small, regular, and bisexual. They are 5-merous except for the pistil, which is bicarpellate. The order of develop-

ment of the floral organs is peculiar, *viz.*: stamens, petals, sepals, and pistil. The calyx may be reduced to a few minute scales or to a narrow circular ridge. The insertion is epigynous.

Fruits and Seeds.—The fruit is characteristic of the family and is called a schizocarp. At the top, where the style was attached, is an elevation, the stylopodium, which is the remains of a nectary. In dehiscence the two carpels, called mericarps, separate, the line of division being called the commissure. For a time

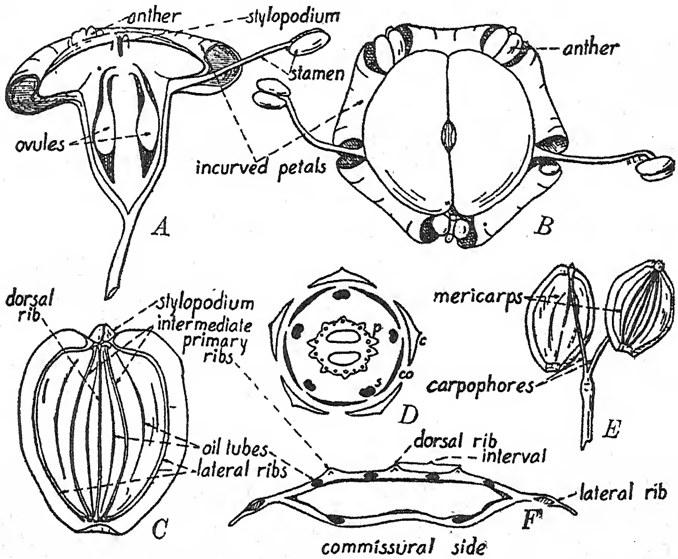


FIG. 72.—*Pastinaca sativa* (Umbelliferae). *A*, longitudinal section of flower. *B*, top view of same. *C*, dorsal view of mericarp. *D*, floral diagram. *E*, fruit. *F*, cross section of mericarp. (*After Robbins.*)

after dehiscence each mericarp hangs suspended by a slender stalk, the carpophore. Each mericarp contains a single seed, which is adherent to it, with the result that the whole structure is commonly called a seed. The fruit is variously marked with ribs, grooves, bristles, and oil tubes, which are much used for generic and specific distinctions. The seed has a hard oily endosperm.

Economic Significance.—The Umbelliferae are important chiefly for vegetables, volatile oils, and drugs. Of the vegetables, carrots, parsnips, and celery are the chief members. The biennial species store much food in fleshy taproots the first year of

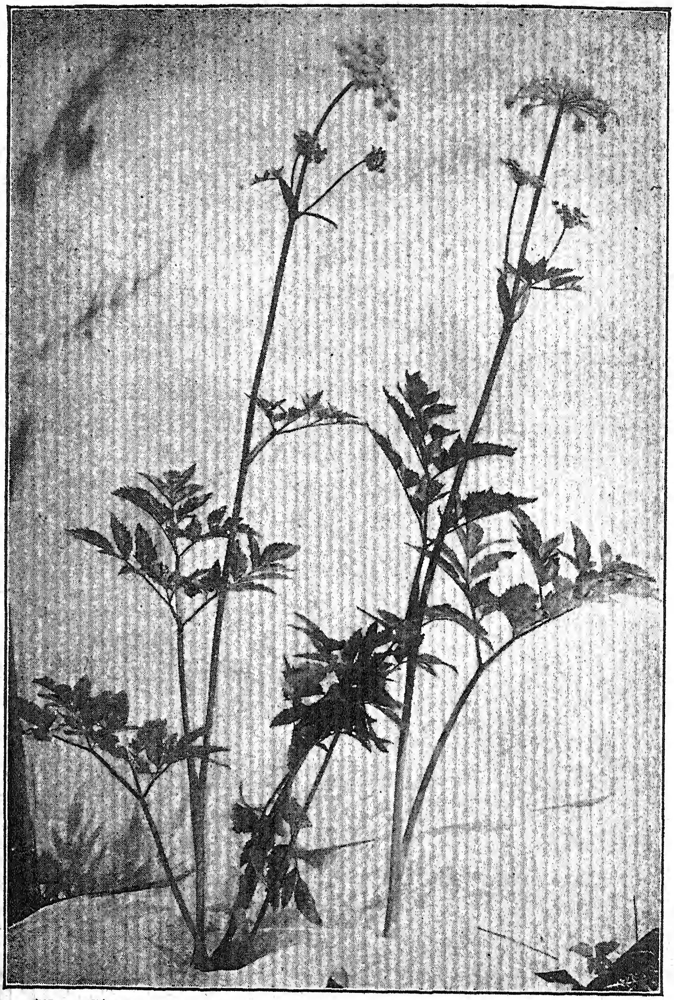


FIG. 73.—*Cicuta occidentalis* (Umbelliferae). Water hemlock or water parsnip. This common name applies to the various species of *Cicuta*, all of which are probably poisonous from the presence of cicutoxin. They are widely distributed and grow chiefly in marshy places and along streams and ditches. (One-eighth natural size.)

their growth, and if these are grown a second season this food is used in fruiting. Volatile oils, resins, etc., are produced in glands in the bark, leaves, and fruits and give the plants their fragrance. Caraway (*Carum Carvi* L.), dill (*Anethum graveolens* L.), and anise (*Pimpinella Anisum* L.) are used for flavoring. Angelica,

carum oil, conium, asafetida, and numerous other medicinal products are obtained from this family.

The family Umbelliferae is one of the most important for forage plants. Among the members worthy of mention are the angelicas (*Angelica* spp.), cowparsnip (*Heracleum lanatum* Michx.), wild parsley or carrot (*Leptotaenia* spp.), and sweetcicely (*Osmorrhiza* spp.). Several species are poisonous. Most important among these is waterhemlock, cowbane or poison parsnip (*Cicuta* spp.), and conium (*Conium* spp.). The fleshy roots of these plants are very deadly to all kinds of livestock and have many times been fatal to man. The poisonous principle is an alkaloid, cicutin. There is a popular belief that, if the common garden parsnip escapes from cultivation, it becomes poisonous. This is an error based on wrong identification. It has been abundantly proven that parsnip run wild is harmless.

46. RUBIACEAE. Madder Family

$$\begin{array}{c} \mathrm{S}^{4-5} \\ \mathrm{CA}^{4-5}\overline{\mathrm{Co}^{4-5}} \\ \hline \mathrm{P}\textcircled{2} \end{array}$$

This is a large family of some 350 genera and 4,500 species. Most species are found in the tropics and subtropics, but a considerable number grow in temperate zones.

Familiar Examples.—In some cases we are familiar with the plants themselves, in others with their products. These include bedstraw (*Galium* spp.), buttonbush (*Cephalanthus occidentalis* L.), madder (*Rubia tinctorum* L.), capejasmine (*Gardenia jasminoides* Ellis), coffee (*Coffea arabica* L.), and quinine (*Cinchona officinalis* Hook.).

Stems and Roots.—The family consists mostly of shrubs and small trees, with some vines and herbaceous plants.

Inflorescences and Flowers.—The flowers are usually solitary or in small axillary clusters. In most species they are regular, in a few slightly irregular, ovary inferior, carpels generally 2 to 5, stamens 4 or 5.

Fruits and Seeds.—The leaves are simple and in most cases opposite or whorled. The stipules are often conspicuous and leaf-like.

Economic Significance.—Some very important products come from the Rubiaceae. The two most important of these are

coffee, obtained from the fruits of the coffee tree, and quinine, obtained from the cinchona bark. The "coffee beans" are seeds, two of which are produced inside each pulpy fruit. The alkaloid quinine, of which the bark sometimes contains as much as 10 per cent, is extracted by mechanical and chemical processes, after which it is easily purified. From the roots of madder an important dye is extracted. A number of species, including cape-jasmine or gardenia, are grown in greenhouses and out of doors in mild climates.

47. CAPRIFOLIACEAE. Honeysuckle Family

$$\frac{S^{3-5}}{\dfrac{\overline{\mathrm{CA}^{\overbrace{3-5}}\mathrm{Co}(\underline{3-5})\text{ or }\mathrm{Coz}(\underline{3-5})}}{\mathrm{P}(\underline{1-6})}}$$

This family consists of about 11 genera and 340 species, found mostly in the Northern Hemisphere.

Familiar Examples.—The honeysuckle (*Lonicera* spp.), elderberry (*Sambucus* spp.), snowberry or buckbrush (*Symphoricarpos* spp.), and twinflower (*Linnaea borealis* L. and *L. americana* Forbes) are familiar examples.

Stems and Roots.—The Caprifoliaceae are predominantly shrubs with a few vines, trees, and herbs.

Leaves.—The leaves are generally simple (pinnately compound in *Sambucus*) and opposite. In some species, *e.g.*, in the *Loniceras*, the sessile pairs of upper leaves have their bases united (connate-perfoliate). Stipules are usually absent, but present in *Sambucus* and a few other genera. A few, such as twinflower, are evergreen.

Inflorescences and Flowers.—The predominant inflorescence is a cyme, but this may be variously modified by suppression of terminal (central) or marginal flowers, or by compounding, as in *Sambucus*. The flowers are bisexual, gamopetalous, and often irregular. They are primarily 5-merous, but the parts may be reduced to two, three, or four. The insertion is epigynous.

Fruits and Seeds.—The fruit is generally a berry, but sometimes a drupe or a capsule. The seed contains fleshy endosperm and a straight embryo.

Economic Significance.—The honeysuckle family ranks very high for ornamentals shrubs, both cultivated and wild. Some of the species of *Sambucus* and *Symphoricarpos* furnish considerable

browse for livestock. Several species of *Symphoricarpos* are important honey-producing plants.

48. COMPOSITAE. Composite Family

$$\frac{S^{\widehat{5}\text{ or }0}}{\dfrac{\mathrm{C{\scriptstyle A}}^{0\text{—}\mathrm{P}}\mathrm{Co}^{ⓢ}\text{ or }\mathrm{Coz}^{ⓢ}}{\mathrm{P}(\overline{\underline{1:2}})\text{ or }0}}$$

The Compositae are generally rated as the largest and highest of all the families of plants. There are at least 850 genera and 15,000 species. They are of world-wide distribution, and different members grow under every ecological condition where flowering plants are found. Some authorities would divide this great family into three—Ambrosiaceae, Cichoriaceae, and Compositaceae or Carduaceae.

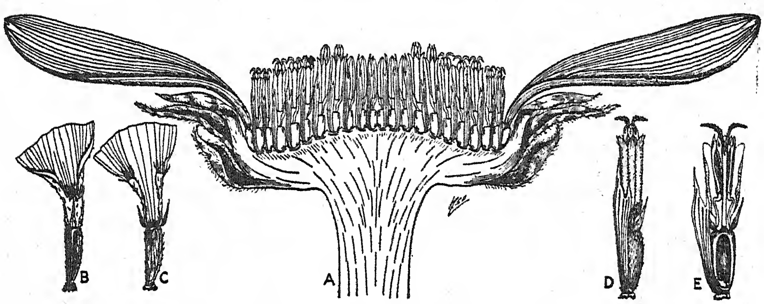


FIG. 74.—Head of sunflower. *A*, longitudinal section of inflorescence showing ray flowers and tube flowers. The older tube flowers toward the margin are fertilized and withered while the younger ones at the center have not yet opened. *B*, external view of ray flower. *C*, interior of ray flower, showing absence of stamens and pistil. *D*, external view of tube flower. *E*, interior of tube flower showing petals, stamens, pistil, and ovule.

Familiar Examples.—Familiar examples are sunflower (*Helianthus annuus* L.), aster (*Aster* spp.), goldenrod (*Solidago* spp.), lettuce (*Lactuca sativa* L.), dandelion (*Taraxacum officinale* Webber), ragweed (*Ambrosia* spp.), chrysanthemum (*Chrysanthemum* spp.), cocklebur (*Xanthium* spp.), Canada thistle (*Cirsium arvense* (L.) Scop.), yarrow (*Achillea millefolium* L.), and wormwood or sagebrush (*Artemisia* spp.).

Stems and Roots.—The Compositae are nearly all herbaceous, but a small proportion are shrubby, and in the tropics a few reach the stature of trees. Tubers are produced by a few species, *e.g.*,

Jerusalemartichoke (*Helianthus tuberosus* L.), and wild artichoke or Maximilian sunflower (*H. Maximiliani* Schrad.). Many species have a milky juice (latex).

Leaves.—The leaves are mostly simple, alternately arranged, and exstipulate.

FIG. 75 —*Eupatorium urticaefolium.* White snakeroot. This plant is found in woods and pastures throughout the eastern half of the United States. (One-half natural size.) (*After Hansen.*)

Inflorescences and Flowers.—The inflorescence is a head subtended by an involucre. It is so compact that the layman usually thinks it is a single flower. The flowers are varied, mostly bisexual, but frequently pistillate or neutral, *i.e.*, with both stamens and pistils aborted, and occasionally staminate. In one type of head (discoid) the corolla is small and regular (tubular) in all the flowers. In a second type (radiate) the central flowers

are tubular, and those in the outer row are ligulate and generally pistillate or neutral. In a third subfamily all the flowers are ligulate. The insertion is epigynous and the calyx teeth are reduced to scales, bristles, or a shallow cup, or they may be entirely absent. The corolla is five-toothed, the stamens usually

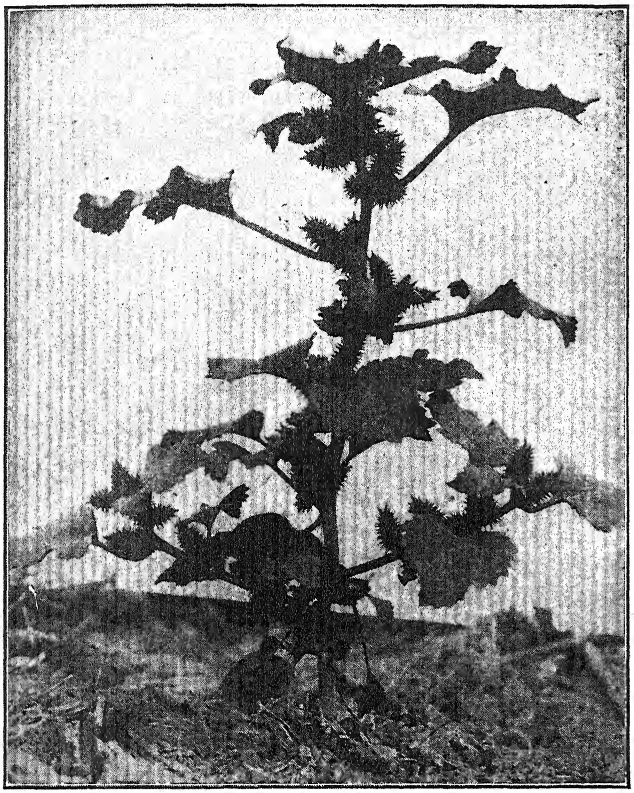


FIG. 76.—*Xanthium echinatum* (Ambrosiaceae). The cockleburs are found most commonly in cultivated fields, waste places, and along the banks of streams where the burs have been deposited by the water. After the plants reach the height of a few inches, they cease to be poisonous. (One-third natural size.)

five in number and connate, and the pistil bicarpellate, with one chamber and one ovule.

Fruits and Seeds.—The fruit is generally a simple achene, which may be naked or plumed from the development of the pappus (calyx). The embryo is straight and there is no endosperm.

Economic Significance.—The Compositae cannot be rated among the highest as a direct source of food for mankind, although lettuce, chicory, artichokes, and salsify make their contributions. A great number of species have considerable forage value, and the cultivated sunflower is excellent for ensilage in regions where corn cannot be grown in quantity. Poisonous members are not generally troublesome, although white snakeroot (*Eupatorium urticaefolium* Reich.), western sneezeweed (*Dugaldia*

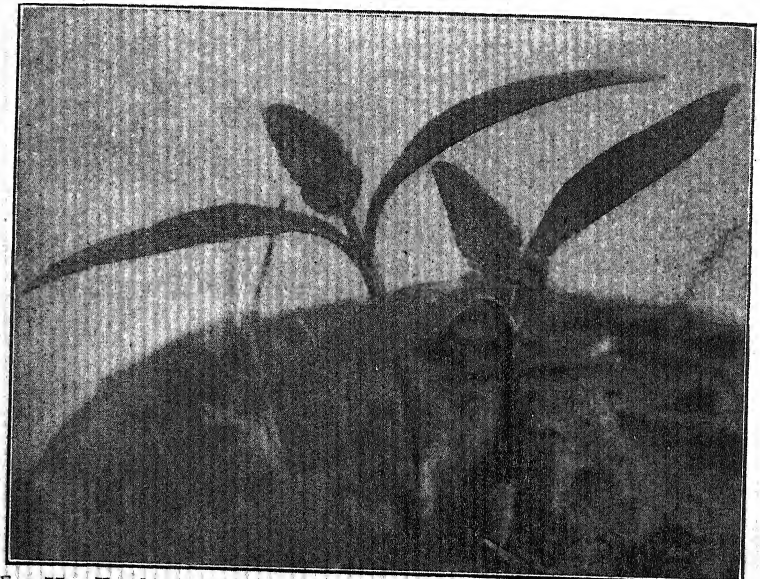


Fig. 77.—*Xanthium echinatum*, Cocklebur. It is at this young stage, while the cotyledons still persist, that the plants are poisonous. (Natural size.)

Hoopesii (A. Gray) Rydb.), some of the goldenrods (*Solidago spectabilis* and *S. concinna* A. Nels.) are known to cause some losses of livestock. Of these, white snakeroot is of the greatest interest as it has been shown to be the cause of the mysterious milk sickness or trembles that affects cattle expecially but may also affect horses and sheep and people drinking milk from poisoned cows. Cocklebur is also important in some sections as a cause of livestock poisoning. The cotyledonous stage of the seedling, which is readily eaten, is poisonous to cattle, but older plants are not relished and are apparently harmless. A considerable number, especially ragweeds (*Ambrosia* spp.) and goldenrods (*Solidago* spp.), are causes of hay fever.

The flower-like heads have given the family a prominent place for decorative purposes. That the great heads of dahlias, chrysanthemums, asters, and daises are thought of as flowers rather then inflorescences does not detract from their beauty. To these names may be added those of the rudbeckias, goldenrods, and a host of wild composites.

In number of official drugs produced the Compositae are among the highest, although these are not of as much value as those of the Solanaceae, for example.

Many species are important as weeds, the worst being Canada thistle, dandelion, cocklebur, sowthistle (*Sonchus* spp.), Chinese and blue lettuce (*Lactuca* spp.), and *Iva* spp.

CHAPTER VIII

FAMILIES OF MONOCOTYLEDONS

In number of families, genera, and species the monocotyledons are not nearly so numerous as the dicotyledons, but certain families, *e.g.*, the Gramineae, are of outstanding importance.

Origin.—The origin of the monocotyledons has been the subject of much controversy. For some years they were thought to be more primitive than the dicotyledons and probably ancestral to them. This belief, however, is out of harmony with both morphological and paleontological evidence. It is now generally conceded that the dicotyledons are the older and gave rise to the monocotyledons. The prevailing belief today is that the monocotyledons were an offshoot of the primitive dicotyledons back in the early part of the Mesozoic era, and that they are monophyletic, *i.e.*, of one origin, the first monocotyledons being ancestral to all others. A third and newer conception is that the monocotyledons are not a simple monophyletic group but are polyphyletic, different members having sprung at different times from distinctly separated representatives of the dicotyledons. The problem has been simplified by Coulter[1] and his associates, who have shown that cotyledons originate, not from a terminal cell but from a "peripheral cotyledonary zone" that may develop one, two, or several cotyledons, or, in a few species, none at all. In both subclasses of angiosperms two generally start, but if growth continues in only one, the embryo is monocotyledonous.

The fact that the two subclasses can, in most cases, be distinguished not only by their cotyledons but also by the venation of the leaves, the arrangements of bundles in the stem, floral structure, and size of the endosperm is evidence of a monophyletic group.

With regard to these other characters, attention has been called to the fact that not all monocotyledons and dicotyledons are typical of their groups in all respects. The atypical struc-

[1] Coulter, J. M., The Origin of Monocotyledony, *Ann. Mo. Bot. Gard.*, **2**: 175–183, 1915.

tures are not, however, characteristic of large groups of monocotyledons or dicotyledons but are quite scattered. Examples are the netted veined leaves of *Smilax*, *Trillium*, and *Arisaema* and the somewhat scattered vascular bundles in the stem of *Thalictrum*, *Peperomia*, *Podophyllum*, and *Nymphaea*.

Description.—The monocotyledons are mostly herbaceous plants, but some (*e.g.*, palms) are large trees. With rare exceptions the leaves have unbranched parallel veins running either longitudinally or from the midrib outward. The embryo has one cotyledon that remains below ground with the endosperm during germination. A second may be present in more or less rudimentary condition. The stem is not divided into bark, wood, and pith, but the vascular bundles, collateral in type, are scattered throughout a soft pith-like parenchyma. The floral parts are usually in threes or multiples of three, *i.e.*, 3-merous. The calyx in many species is colored and corolla-like.

1. ALISMACEAE. Waterplantain Family

$\mathrm{CA}^3\mathrm{Co}^3\mathrm{S}^{6-\infty}\mathrm{P}^{6-\infty}$

These are mostly aquatic plants with simple morphology that places them among the lowest of the monocotyledons and close to

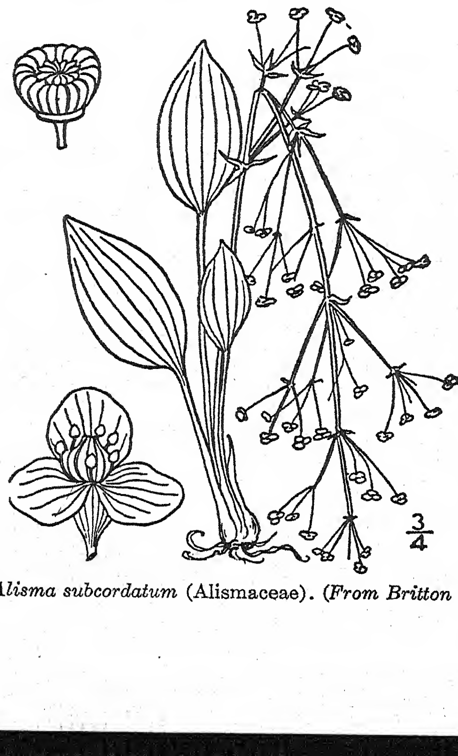


FIG. 78.—*Alisma subcordatum* (Alismaceae). (*From Britton and Brown.*)

the ancestral Ranales. There are only about 14 genera and 60 species, widely distributed in warm and temperate waters.

Familiar Examples.—The best known are the waterplantains (*Alisma* spp.) and the common arrowheads (*Sagittaria* spp.).

Stems and Roots.—The plants are perennial, herbaceous and succulent, growing in marshy places or shallow ponds.

Leaves.—The leaves are simple, mostly entire and often sheathing the stem.

Inflorescences and Flowers.—The flowers are solitary or in whorls. They are trimerous, with three or six stamens and hypogynous insertion. The pistils are unicarpellate and few to many in each flower. The petals are usually white and showy.

Fruits and Seeds.—In most species the fruits are achenes.

Economic Significance.—The plants have some value as ornamentals, being grown in ponds and aquaria. Some species of *Sagittaria* have edible tubers of limited value.

2. LILIACEAE. Lily Family

$$\mathrm{CA}^{3}\mathrm{Co}^{3}\mathrm{S}^{6(3)}\mathrm{P}^{(3)}$$

The lilies and their relatives constitute a large family of splendid ornamental plants. There are about 200 genera and 2,500 species distributed all over the world and very plentiful, both wild and cultivated, throughout the North Temperate Zone. Some authorities would divide this family into three: Melanthaceae, Convallariaceae, and Liliaceae.

Familiar Examples.—Examples are the true lily (*Lilium* spp.), but not the callalily (*Zantedeschia aethiopica* Spreng.), adderstongue or dogtooth violet (*Erythronium* spp.), hyacinth (*Hyacinthus orientalis* L.), tulip (*Tulipa* spp.), lilyofthevalley (*Convallaria majalis* L.), onion (*Allium* spp.), asparagus (*Asparagus officinalis* L.), and Spanishbayonet (*Yucca* spp.). It must be remembered that some dicotyledons with large, showy flowers are called lilies but do not belong in this family.

Stems and Roots.—The Liliaceae are nearly all perennial or biennial herbs, but a few shrubby species of *Dracaena* and *Yucca* are found in the subtropics. In most species the conspicuous underground portion is a bulb or a corm, rarely a rootstock. Many fibrous roots grow from these fleshy portions. In some cases the bulbs or corms serve merely to store food for seed pro-

duction the following year. In others they form in considerable numbers and serve for vegetative propagation.

Leaves.—The leaves of Liliaceae are all simple and parallel-veined, but otherwise they are somewhat variable. In shape they grade from linear to broadly ovate. In some species they are all basal. In others they are alternate, opposite, or whorled.

Inflorescences and Flowers. Various forms of inflorescence are found—racemes, panicles, and umbels—and not a few species have solitary flowers. The flowers likewise are variable, but as a rule they are trimerous and bisexual and have petal-like sepals, equal petals, six stamens, and a tricarpellate pistil with a superior ovary, three seed chambers, and one style with a three-lobed stigma. In many species they are large and beautiful.

Fruits and Seeds.—The fruit is either a berry or a three-chambered capsule with loculicidal dehiscence, *i.e.*, directly into the seed cavities (except in *Calochortus*). The number of seeds varies from few to many. They contain a small embryo within a large endosperm.

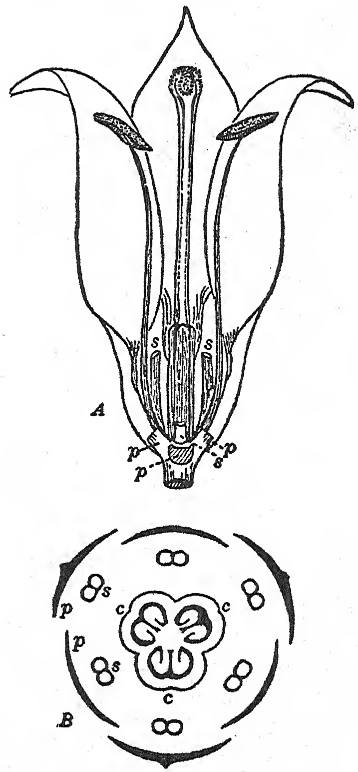


FIG. 79.—*Lilium philadelphicum* (Liliaceae). *A*, longitudinal section of flower. *B*, floral diagram. (*After Bergen and Davis.*)

Economic Significance.—From the esthetic standpoint few families of plants compare with the Liliaceae. The great abundance, variety, and size of the flowers give them much prominence in the greenhouse, flower garden, dooryard, and field. The fact that many of them can so easily be grown from bulbs or corms brings them into the humblest homes and the stateliest mansions. Their use for human food is limited to asparagus and onions. Their forage value is low. They are not troublesome as

FIG. 80.—*Zygadenus venenosus* (Melanthaceae). Death camas. At least four species of *Zygadenus* found from Montana westward and southward are known to be poisonous from the presence of the alkaloid zygadenine. (One-half natural size.)

weeds, but the deathcamas (*Zigadenus venenosus* S. Wats.) should be mentioned as a poisonous weed.

3. JUNCACEAE. Rush Family

$\text{CA}^3\text{Co}^3\text{S}^{3-6}\text{P}$③

The rush family consists of 8 genera and about 300 species of herbaceous, aquatic, often grass-like or sedge-like plants. In reality they are more nearly related to the lilies than to the grasses and sedges, and they are included in the order Liliales.

FIG. 81.—*Juncus lamprocarpus* (Juncaceae). *a*, inflorescence. *b*, single flower. *c*, pistil. (*After Strasburger*.)

Familiar Examples.—Familiar examples are common or bog rush (*Juncus effusus* L.) and woodrush (*Luzula parviflora* (Ehr.) Desv.) but not bulrushes, which belong to the Cyperaceae.

Stems and Roots.—The Juncaceae are all herbaceous and mostly perennial, growing in dense bunches often 1 to 3 feet high. The stems may be cylindrical or angled and contain a soft pith. The roots are fibrous.

Leaves.—The leaves are linear but variable as to thickness. In the larger genus, *Juncus*, the sheaths are split. In the other, *Juncoides*, they are closed.

Inflorescences and Flowers.—Unlike the grasses and sedges, the inflorescences are not made up of spikelets but of single flowers arranged in different ways—racemes, panicles, corymbs, heads, or false umbels.

The flowers in most species resemble in structure a reduced lily. There are three sepals and three petals of similar, broad, greenish-brown scales. The stamens are typically six in number but in some species have been reduced to three, four, or five. The pistil has three distinct carpels and usually three cavities. The general effect of the inflorescence is that of a sedge, olive-green or brownish in color; but close inspection shows a flower structure more like the lilies.

Fruits and Seeds.—The fruit is a tiny capsule containing three seed chambers, or by the omission of partitions only one. Sev-

eral seeds are produced in each chamber. The embryo is small and straight in a fleshy endosperm.

Economic Significance.—Economically the Juncaceae are of little importance. Most species are wholly ignored by livestock, but a few, notably the woodrush, which grows in nonswampy land, are relished.

4. ARACEAE. Arum Family

$$\mathrm{Ca}^{0}\mathrm{Co}^{0}\mathrm{S}^{4-10}\mathrm{P}^{(\boxed{1-x})}$$

The family Araceae contains about 100 genera and 1,500 species, most of which are subtropical or tropical. They tend to be aquatic but some are epiphytic.

Familiar Examples.—The common calla or callalily of greenhouses (*Zantedeschia aethiopica* Spreng.), Jackinthepulpit or Indian turnip (*Arisaema triphyllum* (L.) Schott.), sweetflag (*Acorus calamus* L.), and skunkcabbage (*Symplocarpus foetidus* (L.) Nutt.) are familiar examples.

Leaves.—The leaves are mostly large, simple or compound, usually parallel-veined, but netted in some species, as *Arisaema triphyllum.* In the western skunkcabbage (*Lysichiton kamtschatcensis* (L.) Schott.), they are of enormous size—more than 3 feet long and half as wide. In *Monstera deliciosa* Liebm. of the tropics, sometimes grown in greenhouses, the huge leaf blades are perforated with many natural openings, 1 to 3 inches long by ½ to 1 inch wide.

Stems and Roots.—The Araceae are herbaceous, or the larger forms slightly woody. Some are vine-like and climb by aerial roots. Epiphytic forms are occasionally found in the tropics. Underground stems are usually developed in the form of rootstocks, tubers, or corms, which often have a very pungent taste.

Inflorescences and Flowers.—The striking feature of the Araceae is the inflorescence. This consists of a spadix subtended by a spathe. This entire structure is sometimes of astonishing appearance, being nearly 3 feet long in devilstongue (*Amorphophallus rivieri* Dur.) and colored deep red. In callalily and most other members of the family the inflorescence commonly passes for a flower. The true flowers are unisexual or rarely bisexual. Generally the staminate flowers are at the top of the spadix and

the pistillate below, but some species are dioecious. The perianth is reduced to tiny scales or ridges or is entirely lacking. There are commonly ten stamens or fewer. The single pistil has one to several carpels.

Fruits and Seeds.—The fruit is a berry or utricle. In some species the seeds contain endosperm; in others there is none.

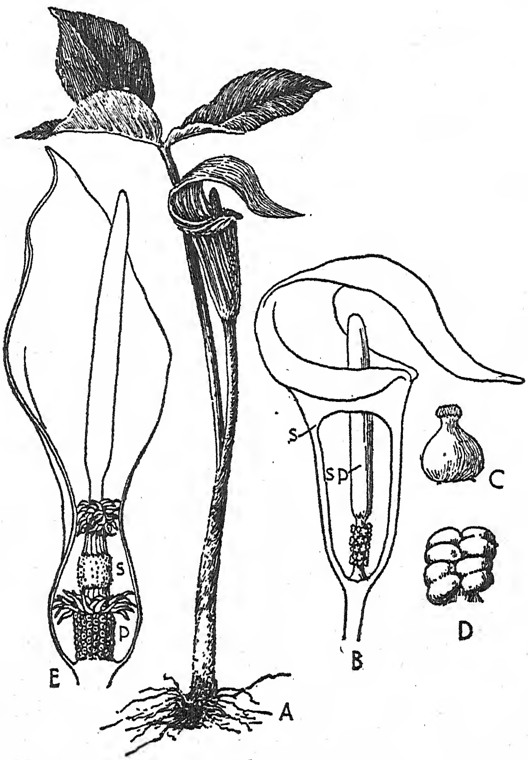


FIG. 82.—*Arisaema triphyllum* and *Arum* (Araceae). *A*, entire plant. *B*, spadix with portion of spathe cut away *C*, pistillate flower. *D*, staminate flower. *E*. inflorescence. *S*, staminate flowers. *P*, pistillate flowers. (*After Curtis.*)

Economic Significance.—General interest in this family is centered in the beauty or oddity of the inflorescence. The corms or tubers are edible in a few species, but they are generally too acrid to be palatable. A few of the members are reputed to be poisonous. The calamus of the drug trade is obtained from the rootstocks of *Acorus Calamus*.

5. PALMACEAE. Palm Family

$$\mathrm{C{\scriptstyle A}}^{3}\mathrm{Co}^{3}\mathrm{S}^{3-6}\mathrm{P}^{③}$$

This is a family of tropical and semitropical trees and shrubs of some 140 genera and 1,200 species. They are naturally of wide distribution, and because of their beauty they have been extended as far into the southern United States as the climate will permit. The smaller species are grown extensively in greenhouses.

Familiar Examples.—The ornamental species are found in several genera, and also we have large interest in the datepalm (*Phoenix dactylifera* L.), the coconutpalm (*Cocos nucifera* L.), raffia (*Raphia ruffia*), and palmetto (*Sabal palmetto* Lood.).

Stems and Roots.—The palms are mostly trees, some of them of great height, but there are a considerable number of shrubs and a few woody vines.

Leaves.—The leaves are persistent, very large in size except on the vines, and either compound or, if simple, deeply cleft and plicate. On the larger trees they form a dense tuft at the top of the unbranched trunk, the basal ones dying as new ones are formed in a huge bud at the top.

Inflorescences and Flowers.—The prevailing inflorescence is a spadix. Some of these are simple, others are in great paniculate clusters with a large spathe covering the cluster during development. The flowers are small and greenish, trimerous, the three carpels usually united and each containing one ovule in most species.

Fruits and Seeds.—The fruit is usually a drupe that develops from one of the three carpels, the other two degenerating. The endosperm is large, especially in the coconut, where it forms the bulk of the edible portion.

Economic Significance.—Most species in use are grown for ornamental purposes, often giving a tropical appearance to the landscape. The value of coconuts and dates is well known.

6. CYPERACEAE. Sedge Family

$$\mathrm{C{\scriptstyle A}}^{0}\mathrm{Co}^{0}\mathrm{Sc}^{1-2}\mathrm{S}^{1-3}\mathrm{P}(\boxed{1{:}2\text{–}3})$$

The sedges, often called sloughgrasses, resemble the true grasses so much that they are commonly mistaken for them. There are about 75 genera and 3,200 species, widely distributed over all parts of the world, but especially abundant in wet soils.

Only about 10 per cent of the species are found in the United States. The sedges are distinguished from the grasses by the following characters, to some of which there are occasional exceptions: (1) angular stems without joints, (2) three-ranked leaves, (3) closed leaf sheaths, (4) only one glume at the base of each flower, (5) perianth composed of bristles or lacking, and (6) seed free from wall of fruit (achene).

Familiar Examples.—Sloughgrass (*Carex* spp.), bulrushes (*Scirpus* spp.), and umbrella plant (*Cyperus alternifolius* L.) are the commonest examples.

Stems and Roots.—The Cyperaceae are practically all herbaceous, annuals or perennials, rarely biennials. The stems are usually solid and without nodes between inflorescence and crown. In the majority of species they are triangular, but in some they are quadrangular, flattened, or cylindrical. The roots are fibrous and fascicled, many of them on perennial species being adventitious from underground rootstocks.

Leaves.—The leaves are mostly linear and grass-like, but the leaf sheath in nearly all species is closed. They have a three-ranked arrangement on the stem. The ligules are absent or very much reduced.

Inflorescences and Flowers.—As in the Gramineae, the spikelet is the unit of structure in the inflorescence. The flower structure differs chiefly in the further reduction of the perianth to a few bristles, and even these may be absent. The flowers have a single glume at the base instead of two as in the Gramineae. They may be bisexual or unisexual. There are typically three stamens but sometimes more or fewer. The carpels are united in the pistil, which has two or three styles or style branches.

Fruits and Seeds.—The fruit is an achene, usually three-angled, containing one seed. This is free from the ovary wall and has a very small embryo and a large soft endosperm.

Economic Significance.—Compared with the Gramineae the Cyperaceae are of limited importance. The grains as a rule are small, few in number, and insignificant. However, many species grow extensively in swampy regions and make good pasturage. Others are too succulent in the spring and too hard and wiry in the fall. This harsh texture is due in part to serrations on the leaves and in part to deposits of silicates in the leaves and stems.

The papyrus, early used for papermaking, belongs to this

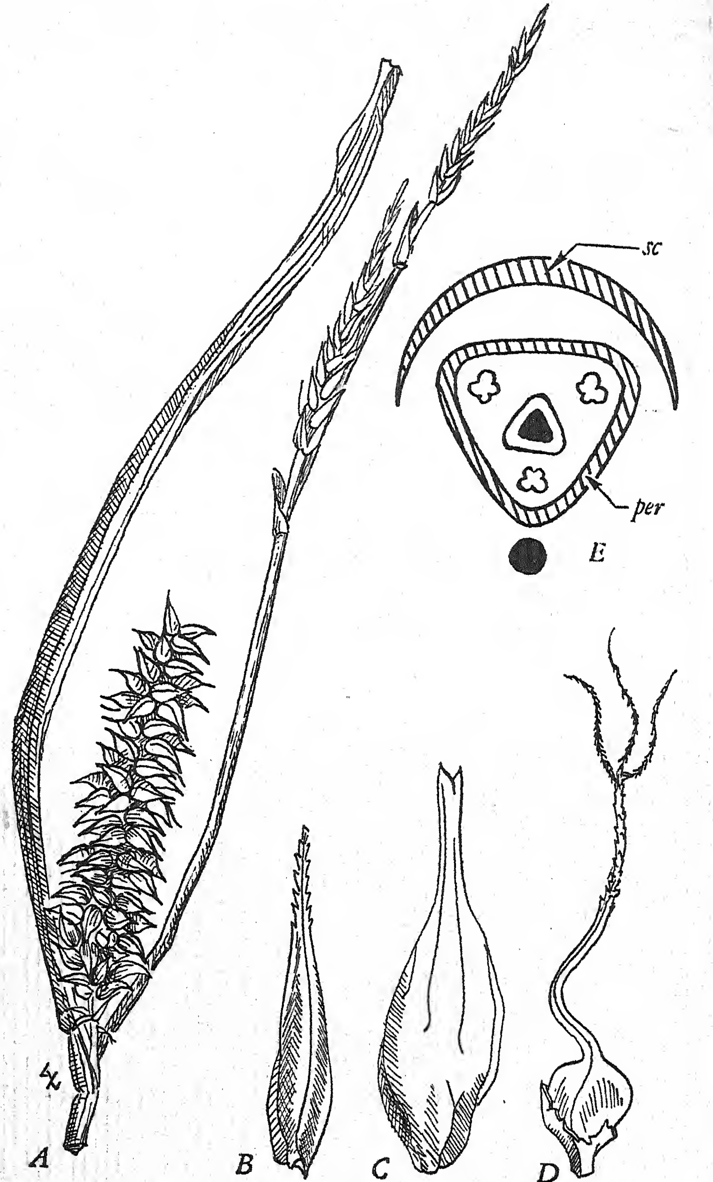


FIG. 83.—*Carex rostrata* (Cyperaceae). *A*, apex of flowering stem with one pistillate and two staminate spikes (×1). *B*, pistillate scale (×8) *C*, perigynium (×8). *D*, achene, continuous with persistent, twisted style and three stigmas (×8) *E*, floral diagram.

family, but it has been largely superseded by straw, linen, and wood pulp.

None of the Cyperaceae is poisonous, and they are unimportant as weeds except where swampy land is cultivated.

7. GRAMINEAE (POACEAE). Grass Family

$$\mathrm{Ca}^0\mathrm{Co}^0\mathrm{Sc}^{2-4}\mathrm{S}^{3(6)}\mathrm{P}\boxed{1:3}$$

The Gramineae constitute the second largest family of monocotyledons, containing about 400 genera and 4,500 species. Of the species found in the United States more than three-fourths are native. The grasses are the most universally distributed, and the most numerous in individuals, of any family of spermatophytes. The great adaptability of the different species has enabled them to thrive under the most varied conditions: in standing water and in deserts, on sun-baked hillsides and in all but the most densely shaded forests, in sand and in gumbo clay, far above the timber line on lofty mountains, and well into the arctic regions.

Fossil remains of grasses have been found in rocks of the Lower Cretaceous period, but in all probability the great diversity of form now found within the family is a relatively recent development. Their simplicity is due to degeneration or specialization rather than to primitiveness. It is probable that the order Graminales should be looked upon as a specialized side branch of the main genetic line of monocotyledons, and as one that has given rise to no other orders.

Familiar Examples.—The well-known members of the Gramineae are too numerous to mention. Representative examples are wheat (*Triticum aestivum* L.), corn (*Zea Mays* L.), oats (*Avena sativa* L.), rice (*Oryza sativa* L.), sorghum (*Holchus Sorghum* L.), sugarcane (*Saccharum officinarum* L.), bamboo (*Bambusa* spp.), timothy (*Phleum pratense* L.), and Kentucky bluegrass (*Poa pratensis* L.).

Stems and Roots.—The grasses are nearly all herbaceous. The prevailing type of stem is a cylindrical culm with conspicuous nodes and hollow internodes, although solid stems are not unusual among the larger members such as corn, sorghum, and sugarcane. Annual, biennial, and perennial species are all numerous. The largest woody species are the bamboos, which may grow to more than 100 feet in height and several inches in

diameter. Among the perennial grasses there is a marked tendency to the formation of rhizomes, underground rootstocks that in some species, such as quackgrass, extend for a considerable distance and serve the function of vegetative propagation. The roots are usually fibrous and fascicled. Small tubers or corms are found in a few species.

Leaves.—Almost without exception the blade (lamina) of the leaf is narrow and ribbon-shaped. The arrangement on the stem is alternate and two-ranked. The leaf is attached to the node by a long sheath, which clasps the stem. This sheath in most species is split throughout its length on the side opposite the attachment of the blade. The union of blade and sheath is usually not a smooth one. Often it appears as if the blade attached slightly below the top of the sheath, and this apparent projection of the sheath above the attachment is called a ligule. It is thinner and more membranous than the sheath proper and is sometimes fringed. The base of the blade at its two margins often projects to form two small ear-like portions called auricles.

FIG. 84.—Spikelet of *Bromus marginatus* showing the glumes and several florets typical of the Gramineae. (One-half natural size)

Inflorescences and Flowers.—The inflorescences and flowers of the grasses are highly specialized, and until their structure has been mastered, they seem difficult to understand. The inflorescences are composed of several to many spikelets, which are combined in various ways on a main axis called the rachis. Some are in compound spikes, as wheat, others are in racemes, as certain species of *Festuca* and *Paspalum*, while still others are in panicles, as oats. It should be understood, however, that the panicles of *Avena*, *Panicum*, etc., are not quite comparable with the panicles of *Yucca*, *Heuchera*, and *Thalictrum*, for example, since in the former each slender stalk bears a spikelet of flowers while in the latter it bears a single flower.

Each spikelet bears one to several *florets* attached to a central stalk or *rachilla*. The usual structure of a spikelet is as follows: At the base is a pair of *glumes*, the lower, outer one called the first, and the upper, inner one called the second. Above the glumes, and partly enclosed by them, is a series of florets. Each

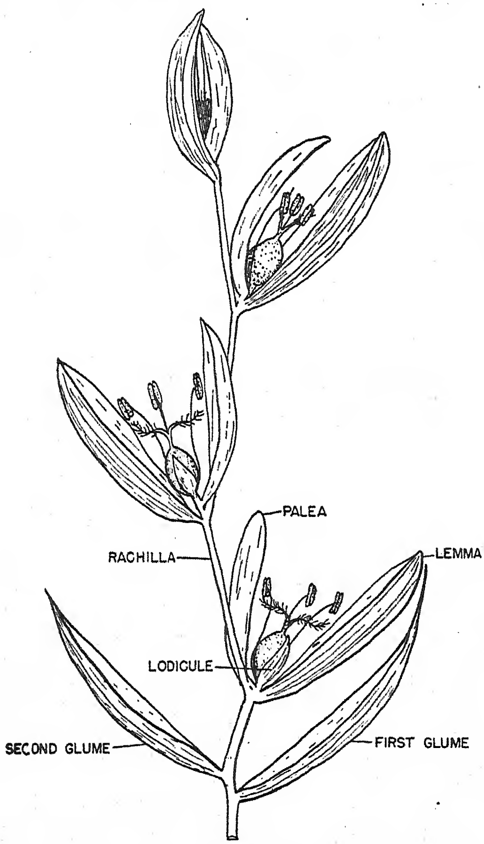


FIG. 85.—Representative spikelet of grass. The rachilla here is elongated to show the parts more clearly.

floret has at its base a *lemma* and a *palea*. The lemma is the lower, outer scale of the floret, which in many species bears a long slender awn or beard as an extension of the midrib at the tip or back. In its axil the floral parts are borne. The palea, often with two longitudinal ridges (*keels* or *nerves*), stands between them and the rachilla. The floral parts consist of a perianth

(sometimes absent) that is reduced to two or three minute scale-like *lodicules*, three stamens (one, two, or six in a few species), and a central pistil of three united carpels, only one of which is functional. The superior ovary bears two (rarely three) feathery stigmas with short styles or none. Many species have other florets on the rachilla, the upper or lower of some being sterile.

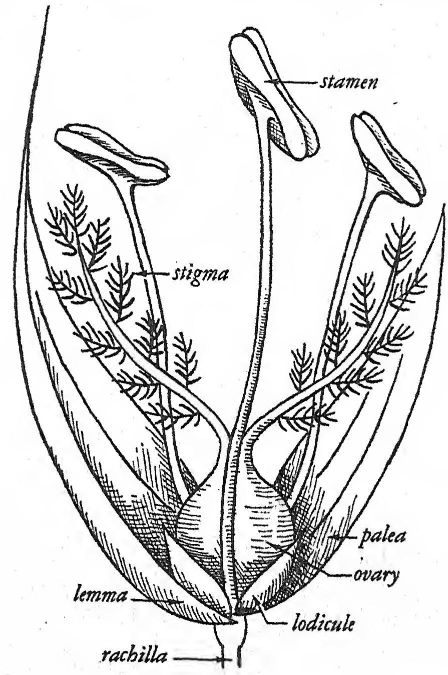


FIG. 86.—Representative floret of grass, much enlarged.

Flower study in the grasses is complicated by the fact that there has been much suppression and modification of floral parts, and this has taken place in varying degrees in different species. The perianth condition of the grass ancestor is unknown, but it is not unlikely that it consisted of two whorls of three parts each. Three lodicules can still be found in some species. There probably were six stamens, this number still being found in bamboo and in rice. The pistil doubtless had three carpels; in fact, studies in the early development of the flowers have shown that this number still persists, although they

are so intimately fused that they appear as one. Three styles, suggestive of as many carpels, are not unusual. In most species the flowers are bisexual, but in corn, for example, the stamens and pistils are in separate flowers. Even here bisexual flowers in the staminate tassels are fairly common. This specialized floral structure furnishes ground for the belief that the grasses are not primitive plants but derivatives of lily-like ancestors.

Fruits and Seeds.—The one-ovulate pistil develops into a hard, dry, seed-like fruit, similar to an achene, but strictly speaking a caryopsis, since the seed adheres closely to the surrounding ovary wall. In some species, such as oats and hulled barley, the palea and lemma continue to enclose the grain after threshing. The

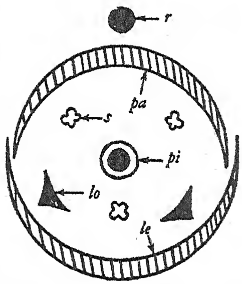


FIG. 87.—Floral diagram of grass. *pi*, pistil. *s*, stamen. *lo*, lodicule. *pa*, palea. *le*, lemma. *r*, rachilla.

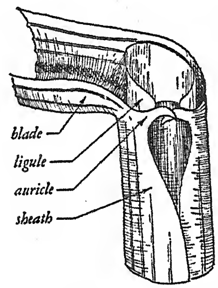


FIG. 88.—Portion of leaf of *Elymus* at the level where the culm emerges from the sheath. (Three times natural size.)

seed is composed largely of starchy endosperm with a relatively small straight embryo near the point of attachment.

Economic Significance.—Undoubtedly the Gramineae excel all other families in their importance to mankind. Without Pinaceae we might live in earthen houses; without cotton we might clothe ourselves in other fabrics; but without Gramineae most of us would starve. Notwithstanding the prevalence of hundreds of other families of plants the earth would support far less animal life were it not for the grasses and grains.

The explanation is not difficult. In the first place, the grasses are abundant; they grow everywhere, under all conditions, filling in the spaces between larger plants and crowding out those that are poorer competitors. In the second place, they withstand injury unusually well, rallying promptly when cut or eaten off. How many other species can withstand steady pasturing by live-

stock or the daily use of the lawn mower? Then, too, they are palatable and nutritious, and practically none are poisonous. The Gramineae furnish summer forage, winter hay, grain for livestock, and bread for man.

Of the different grains, wheat and rice are outstandingly the most important, considering the entire human race, with corn, oats, barley, and rye trailing after.

From the food standpoint we must not overlook sugarcane, which furnishes nearly two-thirds of the world's sugar.

Aside from the food supply the Gramineae have some importance. We in America can hardly appreciate the extent to which bamboo is used in certain parts of the world where timber is scarce. Its great size, strength, and lightness adapt it well for bridges, buildings, furniture, and implements, while much of the waste is used for fuel.

Not even the stately pines or the showy flowers contribute more to the adornment of the earth than do the beautiful carpets of grass that hide her nakedness.

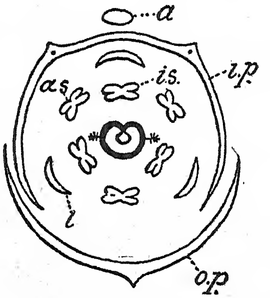


FIG. 89.—*Bambusa* (Gramineae). Floral diagram. (*After Ward.*)

Only a few members of the Gramineae are known to be poisonous, and most of these only under certain conditions. The cyanophilic group, *Holchus* and the closely related *Sorghum*, are the most important of these. Cultivated sorghum, which is a valuable forage plant under normal growing conditions, has caused serious losses of cattle from hydrocyanic acid poisoning during a drought or following a frost. A few other species including sleepygrass, *Stipa robusta*, and stinkgrass, *Eragrostis cilianensis*, are listed as poisonous. Others protect themselves by sharp sawteeth on the margins of the leaves and by spines.

As would be expected among plants so adapted to competition with other forms of life, many pernicious weeds may be found. Notable among these are cheat or chess (*Bromus secalinus* L.), downy brome grass or military grass (*B. tectorum* L.), quackgrass or couchgrass (*Agropyron repens* (L.) Beauv.), wildoat (*Avena fatua* L.), green bristlegrass (*Setaria viridis* (L.) Beauv.), and foxtail barley (*Hordeum jubatum* L.).

COMPARISON OF THREE FAMILIES OF GRASS-LIKE PLANTS

Untrained persons make no distinction between the three common families of grass-like plants. The following table compares these three families. It must be remembered, however, that most generalizations are not without exception.

	Gramineae	Cyperaceae	Juncaceae
Scales.	Glumes, lemmas, paleae	Pistillate and staminate scales, perigynium	None
Perianth . .	0 to 3 lodicules	None or tiny scales or bristles	6-parted Usually scale-like
Stamens . .	1 to 6, usually 3	0 to 3	6, rarely fewer
Pistil	3 united carpels 1 cell, 1 ovule	3 united carpels 1 cell, 1 ovule	3 united carpels 3 cells Several ovules
Fruit	Caryopsis	Achene	Capsule
Leaves	2-ranked, usually with open sheath	3-ranked, usually with closed sheath	2- or 3-ranked, with open sheath
Culms. . . .	Usually cylindrical and hollow, with nodes	Usually angular and solid, without nodes	Usually solid, cylindrical or angular, without nodes

8. IRIDACEAE. Iris Family

$$\frac{\mathrm{Ca}^3\mathrm{Co}^3\mathrm{S}^3}{\mathrm{P}^{\textcircled{3}}}$$

About 60 genera and 1,000 species widely distributed in temperate and warmer regions, becoming fewer northward, constitute this family. That they are among the highest members of the Liliales is shown by their inferior ovaries and reduced stamen number and by the united filaments in *Sisyrinchium*.

Familiar Examples.—The best known examples are the different kinds of iris, flag, or fleur-de-lis (*Iris* spp.), both wild and cultivated, gladioli (*Gladiolus* spp.), and the blue-eyedgrasses (*Sisyrinchium* spp.).

Stems and Roots.—The Iridaceae are all perennial herbs, and most of them have fleshy underground rootstocks, corms, or bulbs.

Leaves.—The leaves are mostly lanceolate or linear, two-ranked, with clasping bases.

Inflorescences and Flowers.—The flowers are mostly large and showy, single or few in a cluster, and subtended by bracts. They are bisexual and usually regular. The perianth is composed of three petal-like sepals and three petals, forming a tube adherent to the ovary. The three stamens are attached to this tube opposite the sepals. The pistil is tricarpellate, with an inferior ovary divided into three chambers. The styles have three branches which are sometimes expanded and petal-like, as in *Iris*, where they add much to the appearance of the flower.

Fruits and Seeds.—The seeds are numerous in a dehiscent capsule. The endosperm is abundant and the embryo is small and straight.

Economic Significance.—Some of the finest of our flowers belong to the Iridaceae. They are also interesting in showing the progress of evolution in the monocotyledons, culminating in the Orchidaceae.

9. ORCHIDACEAE. Orchid Family

$$\frac{\mathrm{CA}^3\mathrm{Coz}^3\mathrm{S}^{1-2}}{\underset{\cdot}{\mathrm{P}}^{3}}$$

The monocotyledons reach the climax of their development in the Orchidaceae. This is the largest family of the monocotyledons and the second largest of all the angiosperms, being exceeded only by the Compositae. Indeed, it is not unlikely that when the tropics have been thoroughly explored the number of orchid species will be placed first among the flowering plants. There are at least 500 genera and 15,000 species, mostly tropical or subtropical but a few growing as far north as Canada. In floral complexity they surpass everything else in the plant kingdom, the specialization being largely to facilitate insect pollination. It is indeed debatable whether or not we are justified in calling the Compositae, the highest of the dicotyledons, more advanced than the Orchidaceae, the highest of the monocotyledons. The Compositae show the greatest advancement in inflorescence, but the Orchidaceae show the greatest advancement in floral struc-

ture, although, as has been pointed out by Bessey, much of the specialization in the Orchidaceae is in the petals, which are the most easily modified of all the floral organs.

Familiar Examples.—Many well-known flowers belong to this family—greenhouse orchids (*Cattleya* spp.), ladyslipper (*Cypripedium* spp.), and coralroot (*Corallorrhiza* spp.).

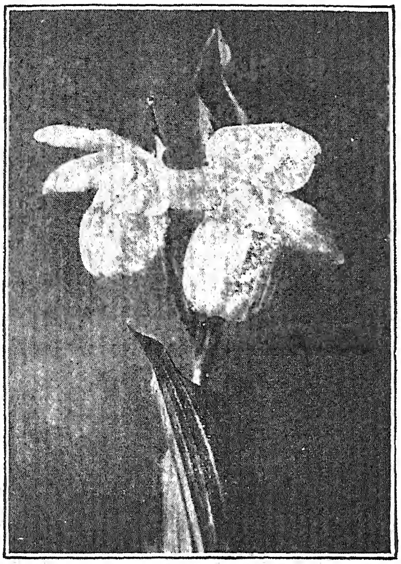


FIG. 90.—*Cypripedium hirsutum* (Orchidaceae). Showing the highly specialized corolla. (*After Sinnott.*)

Stems and Roots.—The Orchidaceae are perennial herbs, mostly terrestrial and green, but a considerable number epiphytic with aerial roots, and a few chlorophyll-less and either saprophytic or parasitic on the roots of other plants. The stems are usually erect but sometimes trailing or climbing. Most species produce fleshy roots, rootstocks, corms, or bulbs.

Leaves.—In most terrestrial and epiphytic species the leaves are fairly uniform except as to width, in which respect they vary from linear to broadly ovate. In saprophytic and parasitic species (*Cephalanthera* and *Corallorrhiza*) they are reduced to scales. Characteristically the leaf bases ensheath the stem. In arrangement they are usually alternate, but sometimes opposite and occasionally whorled.

Inflorescences and Flowers.—In many species the flowers are solitary, but more often they are in racemes or spikes. The flowers are the most remarkable feature of the Orchidaceae. They present so great a variety of detail that only the general plan can be given here. They are bisexual and irregular, *i.e.*, bilaterally symmetrical. There are three sepals, either green or colored to match the corolla, and like each other in appearance.

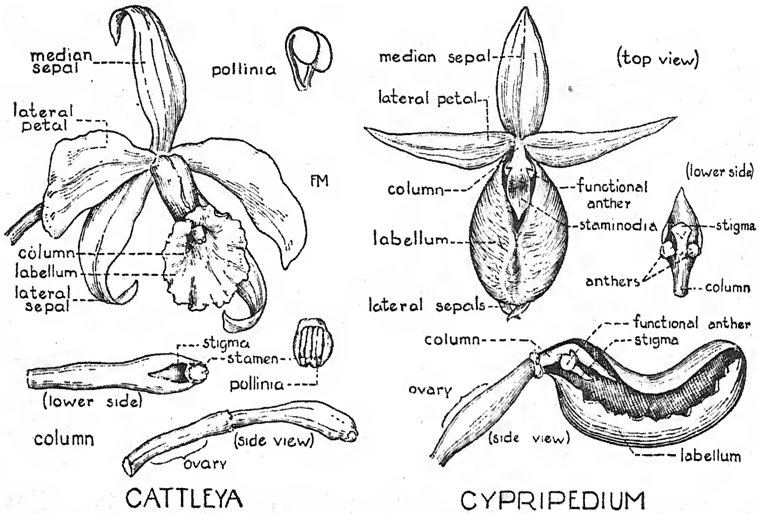


Fig. 91.—The two common floral types found in the Orchidaceae, represented by *Cattleya* and *Cypripedium*. (*Drawings contributed by Florence Mekeel, of the Bailey Hortorium, Cornell University.*)

Two of the three petals are alike or right and left mates and are called wings. The third, below the other two, is unlike the wings, often very much so, being bulbous, spurred, tubular, strap-shaped, or variously branched, and contributing most to the beauty and oddity of the flower. This highly specialized petal is called the lip. The most characteristic part of the flower is the gynandrium or column that is made by a fusion of the three stamens with the pistil. Only one or two of the stamens are functional, and these usually produce two or more stalked pollen masses, pollinia, which are often waxy or even viscid. One lobe of the stigma oftens extends to form a beak—the rostellum. The other two on either side are viscid and functional. These parts of the gynandrium are variously proportioned in

different species, and with the variable lip give endless floral combinations. The pistil is tricarpellate, with an inferior ovary containing one cavity with many ovules.

Fruits and Seeds.—The fruit is quite regularly a three-valved capsule containing many seeds, which are very tiny, with an undifferentiated embryo and no endosperm.

Economic Significance.—The flowers of the Orchidaceae are the most cherished of any in the plant kingdom. Their culture in the greenhouse has become a fine art. In the tropics their remarkable colors, form, and profusion are a constant delight to the traveler. Even in temperate zones the ladyslippers and a few others make an important contribution to the flora.

Unfortunately, the Orchidaceae are sensitive to abuse, and picking the flowers soon exterminates the plants. There are too many people so constituted that their impulsiveness far exceeds their judgment. They cannot seem to learn the relative value of flowers that are growing and those that are picked and wilting. In many sections where ladyslippers were once abundant, they can no longer be found or have become so rare that they are hunted the harder.

COMPARISON OF ORCHIDACEAE AND COMPOSITAE

Since the Orchidaceae and Compositae are generally considered the highest types of the monocotyledons and the dicotyledons, respectively, some useful lessons may be learned by a comparison of the two families shown in the table on page 216.

From this table it may be seen that even the most highly developed plants may be primitive with regard to certain structures. Indeed, more than half of the primitive characters of the angiosperms are illustrated in one or both of these "highest" families.

The relative number of stars in the two columns does not furnish a safe criterion of the relative advancement of the two families, for the characters are not necessarily of equal importance. The student will, however, find it profitable to make similar comparative tables of other families, especially as relationships between families may often be brought out by such comparisons.

	Orchidaceae	Compositae
Habit	*Mostly herbaceous perennials. Many epiphytic and a few saprophytic or parasitic. Often vine-like	Mostly herbaceous annuals. All autophytic and terrestrial. Practically always erect
Stems	*With scattered vascular bundles	With vascular bundles arranged in a hollow cylinder
Leaves	*With parallel venation. All simple	With netted venation. Mostly simple
Inflorescences	Mostly racemes or spikes, but many solitary flowers	*Heads, some of great size
Floral size	*Generally large and showy	Relatively very small
Floral parts	Trimerous; stamens reduced	*Pentamerous; carpels reduced
Insertion	Epigynous	Epigynous
Floral shape	*All irregular—some extremely so	Regular or irregular
Calyx	Well developed and often colored	*Much reduced or wanting
Corolla	Polypetalous	*Gamopetalous
Sexuality	Bisexual	*Bisexual, unisexual, or neutral
Androecium	*Originally of 6 stamens now reduced to 3, of which 1 or 2 are staminodes. United to the pistil. Produce pollinia	Usually 5 stamens which are connate. Produce powdery pollen
Gynoecium	*Tricarpellate, one-chambered. Often greatly modified	Bicarpellate, one-chambered
Pollination	*Entomophylous	Anemophylous or entomophylous
Placentation	Parietal	*Basal
Ovules	Numerous. Anatropous	*Single. Anatropous
Fruit	Capsule	*Achene
Seeds	Without appendages	Without appendages
Endosperm	None	None
Embryo	*Undifferentiated (through reduction)	Straight. Dicotyledonous

* A star is here used to indicate that the condition is more advanced in this family than in the other. In some cases there may be a difference of opinion as to which is the more advanced, especially where regressive development has taken place.

CHAPTER IX

NOMENCLATURE

In a general way the term "nomenclature" is used to cover any system of names or, indeed, the names in use whether or not they follow a system. Using the same names, plants might be classified in various ways or they might not be classified at all.

Relation of Nomenclature to Taxonomy.—Conceivably a system of nomenclature might exist that would be independent of classification. Such a nomenclature would supply a name to each *individual*. In botany this would be quite impossible. As soon, however, as we assert that certain individuals are essentially alike and offer a specific name to the group, we are linking nomenclature with taxonomy; for such a grouping is in itself a recognition of relationship. The binomial system carries us still further into taxonomy, for in it the name not only designates a group of like individuals, the species, but it indicates a larger group, the genus, where related species may be found. In systematic botany, then, nomenclature and taxonomy are inseparable

Names Usually Descriptive.—It is natural that the name given to a plant shall, in a measure, describe it or suggest something or someone connected with it. The name may refer to its appearance, as buttercup; to its habitat, as watercress; to its properties, as chokecherry; or to some person that has been associated with it, as Johnsongrass. Such terms have a meaning only to people familiar with that language, and, indeed, in the evolution of a language the meanings of terms are often forgotten. Dandelion, rose, mullein, yarrow, and huckleberry are doubtfully descriptive today.

COMMON NAMES

Probably all nations and tribes have given names to plants, each in its own language. Such terms are learned in childhood and handed down from generation to generation. They are fairly definite if the plants have no closely similar relatives, as

cowparsnip, white sweetclover, basswood, and sassafras, but are loosely applied among plants having many similar kinds in a group, such as the grasses, willows, huckleberries, and goldenrods. A common name may or may not represent a species in the botanical sense. Sometimes it includes everything within a genus, and it may be the generic name, as *Iris*, with or without a qualifying adjective, as Persian iris. In any event the same name is applied to all plants supposed to be of the same *kind*. No attempt is made to name each *individual* plant except in case of unusual specimens—mostly trees of sentimental value.

The Value of Common Names.—There is a tendency for systematists, especially beginners, to hold common names in contempt. This attitude is natural enough but may be overdone. The common name is generally somewhat descriptive to those using it and is easily learned and remembered because of its familiar sound, even though long, as Jackinthepulpit, dogtooth violet, and bachelorsbutton. In the majority of cases, the approximate accuracy of the name is sufficient for the purposes of the person using it, as pine or elm. If a little more definiteness is desired, an adjective may be added, as yellow pine or slippery elm. It is safe to say that, as a rule, the common name is quite satisfactory to the nontechnical person and more satisfactory than the so-called scientific or botanical name would be. The common name may be monomial, binomial, trinomial, or polynomial.

The Weaknesses of Common Names.—There are three principal defects in common names: (1) They may be quite indefinite. (2) They are restricted to the people of one language or even one section of a country. (3) They are not regulated by any constituted authority.

We now hold that unless a common name is strictly synonymous with the specific name, or in some cases a varietal name, it is too vague for scientific usage. Buttercup, daisy, and goldenrod are familiar examples. In a large country a plant may be called by different names, as pennycress, fanweed, and stinkweed. On the other hand, the same name, as bluebell or bunchgrass, may be applied to several different plants. Such differences in usage are highly confusing, provoke many fruitless controversies, and make the terms wholly unusable for scientific purposes.

To a traveler in a foreign country, the local names encoun-

tered are even more troublesome than botanical names, for they are just as hard to learn and have the disadvantages found in all common names, and if one travels or reads extensively he has many sets of names to learn.

There is no court of last appeal to settle controversies concerning the accuracy of common names. We have, to be sure, a book entitled "Standardized Plant Names" (see page 323), which is a move in the right direction and valuable as far as it goes, but it is far from complete. Most of the lists of common names of wild plants make a free use of synonyms, and if any person or community wishes to adopt a new name for a plant, as has been done hundreds of times, there is no authority to stop it, and the confusion is increased.

BOTANICAL OR SCIENTIFIC NAMES

Every science has developed a terminology of its own, a set of technical terms peculiar to the subject matter of that science. In systematic botany these technical names of plants number many thousands and are far in excess of the common names.

Origin and Nature of Botanical Names.—To get a correct conception of scientific names the reader must understand something of their composition. Many of the older names are Greek in origin but are now used in Latinized form, and the later ones are mostly Latin. The earliest Greek and Latin names were, in reality, the common names used in those countries. At the present time each kind of plant is given a generic name followed by a specific name or epithet.[1] The generic name is a noun, and the specific epithet takes the form of a modifying adjective indicating which of the several members of the genus is being considered.

Generic Names.—The generic name indicates in a general way the kind of plant under consideration. Thus, *Quercus* is the name of all kinds of oaks, *Acer* is the name of all kinds of maples, and *Lupinus* is the name of all kinds of lupines. Some genera are

[1] The most recent code of botanical nomenclature makes a distinction between the *name* of a species, which is the binomial by which it is designated, and a specific *epithet*, which is the last word of the binomial; *e.g.*, *Agrostis alba* L. is the specific name of a certain grass, but *alba* is the specific epithet of that grass. If this distinction comes into general use, confusion will be avoided.

such bold, clear-cut, natural groups that they are easily recognized even by the layman. Examples are pines (*Pinus*), grapes (*Vitis*), and roses (*Rosa*). Others are distinguished from their relatives by more obscure characters and are not easily recognized by untrained persons, who may include plants from different genera under one name, such as goldenrod, bunchgrass, and wild pea. On the other hand, they may give different names to different sections of the same genus, *e.g.*, plum, cherry, etc., for *Prunus*, and pumpkin and squash for *Cucurbita*. The trained botanist has less difficulty recognizing genera than species.

When used in a technical sense the generic name should always begin with a capital letter, but some are also used as common names, such as crocus, iris, spirea, and rhododendron, and when so used they begin with small letters.

Usually the generic name suggests or describes some character of the plant, as illustrated by *Trifolium* (three-leaved) and *Corallorhiza* (coralroot). A few generic names are given in honor of people, *e.g.*, *Linnaea* and *Cogswellia*.

Specific Names or Epithets.—The specific epithet is a qualifying term making it possible to distinguish each member of the genus from the others. Most commonly it is a descriptive adjective, such as *alba* (white) or *vulgaris* (common). It may, however, be taken from the name of a person (*e.g.*, *Besseyi* or *Brittoni*) or from the name of another genus; *e.g.*, *Exoascus Pruni* is the species of a parasitic fungus that attacks trees of the genus *Prunus*.

In botanical nomenclature specific epithets are written with small initial letters with the exception of those that are derived from names of persons or are taken from generic names. In bacteriology and in entomology small letters are used exclusively.

Although there is some defense for the claim that the genus rather than the species should be considered the unit of nomenclature, it is more common in modern taxonomy to treat the species as the unit.

Origin of the Binomial System.—The present binomial system of nomenclature had a long evolutionary development. Cato, in his "De Re Rustica" written about two centuries before Christ, used two names for plants, although he lacked the modern conception of genera made up of several species. Later, two tendencies came in. One was to translate the descriptive Greek

nouns used for genera into Latin, in which language they took the form of two words, *i.e.*, binary generic names. The other was to give a descriptive phrase for the specific name. Both these methods resulted in what have been called polynomials. Brunfels, in the middle of the sixteenth century, changed many binary generic names to single ones, and Dodonaeus, a few years later, followed for the most part binomial usage similar in principle to that of today. Gaspard Bauhin in his "Pinax," a list of some 6,000 plants, written in 1623, used the binomial system even more extensively, though not exclusively.

None of these writers, however, impressed upon the botanical world of his time the desirability of abandoning all practice other than binomial, and works continued to appear having mixed usage—monomial, binomial, trinomial, and polynomial. They did, probably, influence Linnaeus to more fruitful efforts through philosophical discussions of the subject in his "Philosophia Botanica" (1751), and to a general practice of one generic name, and one specific epithet in his "Species Plantarum" (1753), which, however, was sometimes followed by a varietal name.

Advantages of Botanical Names.—Two great advantages are commonly claimed for botanical or "scientific" names: (1) that they are the same among scientific people the world over and (2) that they are uniformly binomial. We shall see presently that, while these two qualities are usually found, there are some exceptions.

The greatest advantage of the botanical name is its exactness. If our present system of nomenclature were perfected, each kind of plant would be called by one binomial name only (aside from its common names), and that name would mean the same species to all botanists. Even now this situation exists with regard to the great majority of plants that have been discovered and named, but in unexplored regions, especially in the tropics, there are many species that have not yet received botanical names, and among those that have been studied the names of a few are still in controversy. While binomials are the rule, a few plants bear varietal or other subspecific names (see page 256), resulting in trinomials.

It is also claimed that the botanical name has the special advantage of being descriptive of the plant. This claim has little force, however, for most common names are likewise

descriptive, and since the majority of botanists today, especially the younger ones, are not skilled in Greek and Latin, they do not appreciate the descriptive value of most of these terms.

A further advantage of the botanical name is that it is governed in some measure by international rules of nomenclature, and many names made in violation of these rules have been rejected.

Disadvantages of Botanical Names.—The usual objection offered to botanical names is that they are so long and hard to learn. In reality the difficulty lies not so much in their length as in their unfamiliar sounds and combinations. *Oxyria digyna* and *Ruellia strepens* are not long names, but most people would think them hard because they are, to them, unfamiliar and meaningless.

Another reason why botanical names will often be unusable to the layman lies in the fact that they require an exact delineation of species; and while some species are clearly defined, with easily recognized characters, others look so much alike that technical skill is required to separate them.

NONVALID NAMES

Many of the names that have been applied to groups of plants have been found unusable for various reasons. Some of these names have been given by excellent botanists who have unavoidably fallen into error; others have been due to the carelessness or crudeness of poorly trained men whose zeal to propose new names has exceeded their ability to apply them.

Synonyms.—By the rules of botanical nomenclature, given later in this chapter, a plant or group can have but one valid scientific name, and no two groups can have the same name. For various reasons, however, many species have received two or more names.[1] In such cases methods have been devised for determining the one valid name, and all the others are classed as synonyms, or, according to certain usages, the term "synonym" is applied to both the valid name and the nonvalid ones. While synonyms are commonest in the designation of species, they may also be found among generic and family names.

[1] According to N. L Britton, "Illustrated Flora," 1st ed., 1896, Vol. I, Introduction, p. viii, some species have been given from ten to twenty names, and "for about 200,000 known species of plants there are not fewer than 700,000 recorded names" or an average of more than three names per species.

Typonyms.—"A name is rejected when there is an older valid name based on the same *type*[1] (typonym)."[2] Typonyms are sometimes called absolute synonyms because the older valid name and the new nonvalid ones refer unquestionably to the same plant or group.

A few examples will serve to make clear the nature of typonyms. In 1894, G. S. Jenman gave the name *Asplenium Guildingii* to a plant, and 3 years later Hermann Christ named the same specimen *A. Vincentis*, thereby establishing a typonym. The generic name *Miegia* given by C. H. Persoon in 1805 is a typonym of *Arundinaria* given by André Michaux to the same species in 1803.

Metonyms.—"A name is rejected when there is an older valid name based on another member of the same group (metonym)." Had the two species mentioned in the preceding paragraph been named from different type specimens, *A. Vincentis* might have been called a metonym. Likewise, *Miegia* might have been regarded as a metonym of *Arundinaria* if it had been based on a different species. The generic names *Bromus*, *Zernia*, *Serrafalcus*, and *Forasaccus* were based on different species. Most authorities consider all these to be the same genus; therefore, *Bromus*, the oldest, is the valid name and the four others are metonyms. *Panicum pilosum* Swarts, *P. distichum* Lam., *P. pilisparsum* Meyer, and *P. trichophorum* Schrad. were named from different specimens, which probably were of the same species. *P. pilosum*, being of the earliest date, should be regarded as the valid name and the rest as metonyms.

It will be noted that personal opinion may enter into the determination of metonyms, for one taxonomist may regard the plants to which these names have been given as all one species, notwithstanding very slight differences in them, while another may think these differences are great enough to justify different specific epithets. Such cases are rare, however.

Metonyms and typonyms have arisen in several ways. In early days the seriousness of duplicate names was not appreciated.

[1] The term "type" as here used applies to the individual plant or plant group that was used as a basis for the description of the species or higher category (see p. 231).

[2] This quotation and those defining metonym, homonym, and hyponym are taken from the American Code of nomenclature (see pp. 230 and 312). Although this code is no longer used, the terms are very convenient.

Botanical names up to the sixteenth century had somewhat the same stability that common names have today. If a botanist happened to know the name by which a plant was designated, he generally used that name. If not, or if he did not like the name in use, he proposed another. Furthermore, the name given a plant was not always published with a description of the plant, as is the custom now. Since the time of Linnaeus a serious effort has been made to follow the names in use rather than to apply new ones. This is often difficult to do. Many names and descriptions have been published in obscure books, journals, and pamphlets, in various languages. Occasionally, also, two names have been published so nearly simultaneously that the first was not distributed to the botanical world until the second had been entered for publication. Furthermore, some botanists have not been careful to look up established names before proposing new ones.

Sometimes the author of the earlier name gave the plant an imperfect description, and a later worker, seeing the same species in a different environment, believed he had found a different species and gave it a new name. In the lower plants, especially the fungi, different stages in a life history have given rise to different names. Thus, *Fusicladium dendriticum*, representing the conidial stage of the apple-scab fungus, is a synonym of *Venturia inaequalis*, the ascospore stage of the same fungus. The uniting of two differently named groups erroneously supposed to be distinct will always result in synonyms.

Homonyms.—"A name is rejected when preoccupied (homonym)." The same name cannot properly be applied to two different groups. If this is done, the name is a homonym for every group to which it is applied except the first. In the binomial system the full name of a plant is the genus (noun) with the species (qualifying adjective). Therefore, it is permissible to use the same specific name in different genera, as *Quercus alba*, *Melilotus alba*, and *Chenopodium album*. Likewise it is permissible to use the same generic name with different specific names, as *Pinus flexilis*, *Pinus ponderosa*, and *Pinus sylvestris*. It is not, however, permissible to use the same generic and specific combination for plants of different species. *Asarum macranthum*, *Phaca villosa*, and *Vitis virginiana* are among the numerous names that have been thus misapplied. Neither is it permissible to use the same generic, family, or ordinal names for different groups. For

example, the generic name *Setaria* has been applied to lichens (1803) and to grasses (1812). In such a case the name is valid for the first group to which it was applied but a nonvalid homonym in its later application.

Most homonyms have arisen in this way: A botanist studying a species or other group that he believed to be new applied to it a name that was descriptive but had already been used, unknown to him. Since names are not completely descriptive of plants but rather suggestive of a conspicuous character, it is not surprising that the same name should fit two unrelated groups. Indeed, the same name has been appropriately applied to both a group of plants and a group of animals, as *Cereus* for a cactus and a sea anemone and *Hystrix* for a hedgehog and a grass.

It should be understood that a slight difference in the spelling of a word does not necessarily make it a different word. Such a difference may be due to a typographical error, to a contraction, or to the grammatical necessity of making the specific name in Latin correspond to the generic name. For example, *Astrocarpus* is a contraction of *Asterocarpus*, and *albus*, *alba*, and *album* are, respectively, masculine, feminine, and neuter forms of the same adjective meaning white.

Hyponyms.—"A name is rejected when the natural group to which it applies is undetermined (hyponym)." When a name is first applied to a group, the group should be so described, or illustrated, or referred to preserved plants, that its identity can be recognized by other botanists. A name not so described or identified is a hyponym and nonvalid for the group for which it was intended. Names used with no descriptions are designated as *nomina nuda;* those with unsatisfactory descriptions, as *nomina subnuda* or *ambigua*. It is sometimes a matter of opinion whether or not a name has been sufficiently defined. The description, illustration, or other means of identification may be rather poor so that one botanist will think it usable and another will reject it. The generic name *Aragallus*, though classed as a hyponym by some authorities, is used by others. *Adodendrum* Necker and *Calesian* Adams are generic hyponyms, and *Gentiana hybrida* Raf. and *Lechea furfuracea* Raf. are specific hyponyms.

Validity versus Legitimacy of Names.—A distinction should be made between terms that are in common use for branding names as correct or incorrect. Validity refers to whether or not a

name conforms to *all* the rules of nomenclature. A name that is in harmony with all the rules is valid and is the correct name for use. If it fails to conform to any one or more rules, it is invalid or nonvalid. Typonyms, metonyms, homonyms, and hyponyms are all nonvalid. Legitimacy refers only to whether or not a name has been accompanied by a suitable published description, or referred to a type specimen. If so, it is legitimate whether or not it conforms to the other rules. If not, it is illegitimate. The term applies to hyponyms (*nomina nuda*, *nomina subnuda*, and *nomina ambigua*). It follows that all valid names are legitimate, but not all legitimate names are valid.

Dividing and Uniting Groups.—When deeper investigation shows the desirability of dividing a species or other group, the original name is retained by the branch that contains the oldest named member, and a new name is proposed for the other branch. For example, the generic name *Prunus* was at one time used for both plums and cherries. Some have thought it desirable to divide the genus, and since *Prunus domestica*, a plum, was the original species on which the genus *Prunus* was based, the plums retained the name *Prunus* and those cherries that were placed in a new genus were given the name *Padus*.

When two or more genera or other groups are found to be identical in composition and to differ only in name, they are united under the oldest valid name, and the others become metonyms, as in the case of *Bromus* on page 223.

From the foregoing discussion of nonvalid names it will be seen that typonyms and metonyms represent two different kinds of synonym, and, furthermore, that homonyms and hyponyms result in the formation of synonyms, for these names must be replaced by usable terms, leaving them as synonyms.

CITING AUTHORITY FOR NAMES

With so many nonvalid names in botanical literature it is often difficult to determine valid ones. The confusion is somewhat lessened by giving the name of the author (usually abbreviated) immediately after the binomial. This designation of the author is, in fact, considered a part of the full name of the plant and follows the specific epithet with no intervening punctuation mark, as *Lilium canadense* L. and *Mertensia virginica* (L.) DC. In a few cases the binomial is followed by a varietal name, and in such

cases the latter should be followed by the name of the author also, as *Portulaca oleracea* L. var. *sativa* DC.

The correct generic and specific name and authority are usually derived from the array of synonyms as follows: By an examination of the plant it is found that it belongs to a certain genus and that several specific epithets have been applied to it. In most cases the first specific epithet under which it was described is the valid one, even though it was not originally placed in the correct genus.[1] If the plant was first named correctly as to both genus and species, the name of the author follows without parentheses. For example, Linnaeus correctly applied the name *Lilium canadense* L. If, however, a botanist when naming a plant placed it in the wrong genus, the error must later be corrected, in which case it will retain its earliest valid specific epithet when changed to the proper genus. The name of the one who first gave the specific epithet (in the wrong genus) will follow in parentheses and the name of the one who first gave the correct generic and specific *combination* will come afterward, not in parentheses. *Mertensia virginica* was first called *Pulmonaria virginica* in 1753 by Linnaeus, and in 1846 de Candolle showed that it belonged to the genus *Mertensia*, hence the name *Mertensia virginica* (L.) DC. A few other examples will serve to show how specific synonymy is determined.

1. Linnaeus' "Species Plantarum" in 1753 gave the name *Glecoma hederacea* to a plant. In 1834 Bentham named the same species *Nepeta Glechoma*, and in 1888 Britton, Sterns, and Poggenburg named it *Nepeta hederacea*. Linnaeus was the first to give it a legitimate specific name, and if he placed it in the correct genus, its name should stand as *Glecoma hederacea* L., and those proposed later should become nonvalid synonyms.

2. In 1824, Bigelow named a species *Lactuca integrifolia*. This proved to be a homonym, however, for in 1818 Nuttall had applied the same name to a different species. This species of Nuttall's is now correctly known as *Lactuca pulchella*, and therefore *Lactuca integrifolia* is a nonvalid synonym for it. Nevertheless, because it was applied to *Lactuca pulchella* before it was

[1] By agreement botanists do not go back of Linnaeus' "Species Plantarum" (1753) to establish priority in the publication of names, and for some of the groups of lower plants later dates of priority have been set (see p. 230).

applied to Bigelow's species, it cannot be used for the latter, or indeed for any species. For this reason Ellis proposed a new name, *Lactuca sagittifolia*, for the species that Bigelow had incorrectly named *Lactuca integrifolia*.

3. In 1828, Nuttall called a plant *Nuttallia involucrata* but did not give it a specific description. This name, therefore, was a hyponym (*nomina nuda*) and nonvalid. In 1838, Torrey and Gray named the plant *Malva involucrata*. Ten years later Gray decided that the plant belonged to genus *Callirrhoe*. Its correct name is therefore *Callirrhoe involucrata* (T and G.) A. Gray.

4. In 1753, Linnaeus' "Species Plantarum" gave the name *Arnica montana* var. *alpina*. In 1799, Olin and Ladin did away with the trinomial by giving the varietal name a specific value, and the plant is now known as *A. alpina* (L) Olin and Ladin. They were not required to use the name *alpina*, however, since varietal names are not protected by priority.

EFFORTS TOWARD UNIFORMITY

Realizing the confusion that is produced by the use of nonvalid names and the uncertainty as to what should constitute validity, botanists have made repeated efforts to reach a common basis. These efforts have taken the form of comprehensive publications, such as Linnaeus' "Genera Plantarum" and "Species Plantarum" and Bentham and Hooker's "Genera Plantarum," and meetings have been held to establish principles and rules governing nomenclature.

Botanical Congresses.—Linnaeus in 1751 proposed a few rules dealing mostly with generic names. Since that time the number of congresses, national and international, that have been held to reach agreements on nomenclatorial and taxonomic procedure has been much greater than is generally realized.[1]

The Paris International Congress.—In 1866 a group of eminent taxonomists met in London to discuss ways and means of standardizing botanical nomenclature. No rules were formulated but they authorized the French taxonomist, A. P. de Candolle, to draw up a set of rules of botanical nomenclature and present them to a congress to be held in Paris the following year. As passed by that congress, they were made up of principles, rules, and proce-

[1] See Herbert C. Hanson, Codes of Nomenclature, and Botanical Congresses, *Amer. Bot.*, **21,** 114–120, 1925.

dures[1] that were highly constructive but conservative and consisted mostly of those that had been tried out and found satisfactory. Arbitrary and untried regulations were wisely avoided. The following provisions, among others of less significance, were adopted: (1) A plant can have but one valid technical name. (2) A species is not named unless its specific name is assigned to a genus. (3) The name must be accompanied by a description, or other means of identification, with date. (4) Two different species, or other groups, cannot bear the same name. (5) Generic and specific combinations should be followed by the name or names of their authors. The Paris Code, as it has been called, also clarified and to some extent unified the use of categories for taxonomy and threw strong emphasis on the desirability of Latin names.

While criticism has been made of some of the provisions of the Paris Code (not those given above), it has had a great permanent value, and it became the basis of all work of this kind that followed it at later congresses.

The Vienna International Congress.—In 1905, after the Paris Code had been given a thorough trial, the second International Botanical Congress met in Vienna. In general the principles and rules of the Paris Code were readopted, but many slight changes in wording were made as a result of experience in applying that code. The Vienna Code made the following notable changes: (1) The use of Linnaeus' "Species Plantarum" (1753) as a beginning point for priority of names was limited to vascular plants. (2) Recognition was given to Linnaeus' "Genera Plantarum," fifth edition, published in 1754, for generic names. (3) Names that had been rejected for certain reasons could in the future be applied as new names to other groups. (4) Any new name was to be nonvalid unless a Latin diagnosis or description of the group was published with it, this provision to go into effect January 1, 1908. (5) A list of *nomina conservanda*, or names retained although not valid under the rules, was authorized. These were mostly generic names that had come into prominent use either before the adoption of the Paris Code or in violation of it. Unfortunately, the list of such names was large and adopted hastily, and the selection was not based on the mature judgment of a representative group of botanists from all countries. No provision was made for adding to the list when older obscure names

[1] For the English translation of the rules in full, see *Amer. Jour. Sci.*, **45**: 63–77, 1868.

are found, which, by a strict application of the rules, would invalidate names in general use. The code was published in French, English, and German.

The Brussels Congress.—In 1910, the third International Botanical Congress met at Brussels. By this time it was realized that, since Linnaeus had given relatively small attention to the lower plants, it would be wise to use the work of other men specializing in these groups as beginning points for establishing priority in some of them. This the Brussels Congress did,[1] and it also made minor improvements in the wording of several of the rules of the Vienna Congress. The two were published jointly in 1912 (see page 312) and became known as the International Rules.

American Contributions.—The American botanists working through the botanical section of the American Association for the Advancement of Science have long taken a progressive attitude toward unified nomenclature. At a meeting in Rochester, New York in 1892 they set up a code that emphasized priority in determining the validity of names and specified Linnaeus' "Species Plantarum" as the starting point for such priority.

In 1903, this organization appointed a nomenclature commission, which, at a meeting in Philadelphia in 1904, approved a code for submission to the Vienna Congress. It introduced the "type concept," which is, briefly, that each species shall be based on a type individual, each genus shall be based on a type species, etc. This idea was rejected by the Vienna Congress. In protest against the *nomina conservanda,* as adopted by the Vienna Congress, and the requirement of a Latin diagnosis to accompany the names of new groups, and because of the cold reception given to

[1] In these rules the starting points for priority for the specific names of the different groups of plants were as follows: For Spermatophyta, Pteridophyta, Sphagnaceae, Hepaticae, Lichenes, Myxomycetes, and Algae (with the exceptions given below) Linnaeus' "Species Plantarum" (1753). For Musciniae, Hedwig's "Species Muscorum" (1901). For Nostocaceae Homocysteae, Gomont's "Monographie des Oscillariees" (1893–1899). For Nostocaceae Heterocysteae, Bornet and Flahault's "Revision des Nostocacees Heterocystees" (1886–1888). For Desmidiaceae, Ralf's "British Desmidieae" (1848). For Oedogoniaceae, Hirn's "Monographie und Iconographie der Oedogoniaceen" (1900). For Uredinales, Ustilaginales, and Gasteromycetes, Persoon's "Synopsis Methodica Fungorum" (1801). For other fungi, Fries' "Systema Mycologicum" (1821–1832). For all fossil plants, the date 1820.

some of the valuable ideas of the American representatives, particularly the type concept (see below), an American Code[1] was set up in 1907. For some time thereafter usage among American botanists was divided, some following the Vienna Code and others the American Code.

The use of two codes in America has resulted in much confusion and difference in the manuals, which is unfortunate. Probably a uniform following of the International Rules would have served our purpose better up to the present time, but it was hoped by some that the perpetuation of the American Code would finally result in an improvement of the rules through a future compromise.

THE TYPE CONCEPT

One of the most valuable proposals of the American Committee to the Vienna Congress was the *type concept*, which that congress rejected but which was later adopted.

The type concept embodies a useful principle that is often misunderstood because of the name. Its fundamental purpose is to associate each specific name and description with a definite preserved specimen or specimens, each generic name and description with a named species, and each higher category with a definite member of a lower category included under it. Most attention is given to type species and type individuals. In the selection or designation of types, priority is intended to rule wherever possible, *i.e.*, the specimen that was used in defining a species becomes the type specimen of the species, and the species that was used in defining a genus becomes the type species of the genus.

It is unfortunate that the idea was not conceived under a different name, for morphological types representative of a group have been recognized and must still be recognized, and physiological or serological types are well established in certain groups of fungi and bacteria. Both these are based on *qualities* and are not likely to be identical with nomenclatural types based on *priority*. A morphological type chosen for its representativeness and a nomenclatural type chosen by priority are confusing.

The confusion comes largely through the use of the word "type," which has more than one meaning. It should be under-

[1] See *Torrey Bot. Club Bul.*, **34**, 167–178, 1907.

stood that the reference here is to a *nomenclatural* type—a definite entity with which the name is associated to prevent its being merely a detached conception. The type concept is not an effort to select a *typical* member of the group, although, quite naturally, the type specimen or group is usually somewhat representative. The term "original specimen" rather than "type specimen" has been suggested and used by some European botanists but not by Americans.

Value of the Type Concept.—The strength of the type concept lies in having a definite entity, a plant or a group of plants, rather than a mere written description, for a guide. Such descriptions are admittedly imperfect in that they express only certain qualities that appeal to the author and leave much unsaid. Also, in dividing groups the nomenclatural type indicates what shall remain in the original group, which will retain the original name instead of taking the new one.

It should here be emphasized that the type concept is an addition or supplement to the principles found in the International Rules and the American Code rather than a substitute for them.

The "Type-basis Code"[1] is largely an American conception and was published in 1918 without adoption by any botanical society. It has since been embodied in the International Rules.

Classification of Type Specimens.—To determine which are the type specimens that were used as a basis for the names and descriptions of the thousands of species named before the type concept was conceived (about 1900) has been a herculean task. These specimens were stored in herbaria the world over, and their labels did not usually specify their peculiar character and value. Through much research a great many of them have been found and identified with the original specific names. Many others are either hopelessly lost, or their identity as type specimens cannot now be determined.

In recent years the custom has been growing of preserving, labeling, and even of distributing to prominent institutions the type specimens used for naming and describing new species. Obviously a single lone specimen, preserved in one herbarium, does not fill the needs of all the botanists who desire to see it, for the shipping of perishable specimens for inspection is a risky pro-

[1] See *Science*, **49**, 333–336, 1918.

cedure, and travel to study these type specimens is expensive and time-consuming.

In making use of the type concept several kinds of types are now recognized.

1. *Type Specimens*, in their simplest and most satisfactory form, are the ones (or the single one) used by the author of a name as a basis for the name and description of a species and designated by him as the type specimen. Since the type concept has been in force, such specimens are usually conspicuously marked and preserved with especial care. Specimens that were used in the description of species in earlier times are often recognizable either by the fact that they were mentioned in the original description of the species or by other means; for example, they may be the only ones preserved by the author of the name, although not mentioned by him in the description.

2. *Isotypes* are duplicate specimens collected by the same person, on the same day, in the same locality, and as nearly equivalent as possible to the type. They may be widely distributed to different herbaria. "Cotype" is an unsatisfactory synonym.

The term "authentic material" has been suggested for plants that differ from isotypes only in date of collection or some other minor respect.

3. *Cotypes* are plants that were in a different collection from that which contained the type specimens but were also used in writing the description. The term is not a proper synonym for "isotypes."

4. *Lectotypes* are the specimens not designated as types by the one who gave the name and description but chosen later as best representing the species—in reality a substitute for the real type that has been lost or is unknown.

5. *Paratypes* are specimens that formed a part of the original collection used in describing a species but were later removed from it.

A much more elaborate classification of types has been proposed,[1] but it seems doubtful that it will come into general use.

The Ithaca Congress.—In 1926, an International Botanical Congress convened in Ithaca, New York, for the consideration of a wide range of botanical subjects, including nomenclature.

[1] FRIZZELL, D. L., Terminology of Types, *Amer. Midland Nat.*, **14**: 637–668, 1933.

Since it was not attended generally by European botanists, it did not enact any legislation in this field but made important progress by the appointment of an interim committee, representing the botanical world, to receive suggestions and make recommendations to the next International Congress, to be held in London in 1930. It was hoped that a revised code could then be agreed upon that would include the best in the three just discussed.

The London Congress.—Following the plan agreed upon at Ithaca, the fifth International Botanical Congress convened in London in 1930. This congress, like the one at Ithaca, covered a broad field, and the section on nomenclature gave detailed consideration to the report of the interim committee.

The phraseology of the rules was improved, and they were clarified in many particulars. All of the more important rules of the Vienna Code were retained, either intact or in slightly modified form. The requirement of a Latin diagnosis for new groups was made to apply to names proposed after 1931 A list of additional *nomina conservanda* was referred to a committee for action. The type concept was definitely incorporated in the rules.

The Amsterdam Congress.—The last International Botanical Congress that has been held met in Amsterdam in 1935. Like the two preceding it, this congress was devoted to the reading of papers in practically all fields of botany. In the field of nomenclature it accepted the rules of the London Congress of 1930 with minor changes and additions. The starting date for the requirement of a Latin diagnosis to accompany new groups (with the exception of bacteria and fossil plants) was changed from January 1, 1908 (Vienna Code), to January 1, 1935. The principle of *nomina conservanda* for species was rejected. The interim committee appointed to act upon suggestions offered them reported the rejection of many and the acceptance of a few minor ones. A special committee was appointed to consider additions to the *nomina conservanda*. On the whole few changes were made.

DIGEST OF RULES OF BOTANICAL NOMENCLATURE

The rules and recommendations of botanical nomenclature, as amended by successive International Congresses, have become too long and complicated, with their qualifications and excep-

tions, to be included here,[1] but a digest of the most important ones is submitted instead.

1. Each plant can have but one valid scientific name.

2. This name shall be binomial, consisting of the generic name followed by a specific epithet.

3. If two or more names have been given to a species, the valid one is the earliest epithet proposed that is in harmony with the rules (but not earlier than Linnaeus' "Species Plantarum," 1753), preceded by the name of the genus to which the plant belongs.

4. When used in a technical sense, as in a specific name, the initial letter of the generic name should be capitalized, but the initial letter of the specific epithet should not be capitalized unless it is derived from the name of a person or from a generic name.[2]

5. The full specific name of a plant includes the name of the author or authors who established the binomial, following the specific epithet.

6. Two different species of plants cannot bear the same binomial combination.

7. To be legitimate a name must be accompanied by a suitable published description. Dating from January 1, 1935, this description or "diagnosis," except in the case of bacteria, must be written in Latin.

8. From January 1, 1912, the name of a new taxonomic group of fossil plants is not considered as validly published unless it is accompanied by illustrations showing the essential characters, in addition to the description, or by reference to a previously published illustration.

9. A name that has been rejected for one kind of plant or group as being a homonym may not later be applied to another kind of plant.

[1] For a complete statement of these rules see A. B. Rendle, "International Rules of Botanical Nomenclature," pp. 1–26, Gustav Fischer, Jena, 1935.

[2] This rule is followed in this textbook and in most botanical manuals. However, in the United States and to some extent elsewhere, there is a strong sentiment in favor of using small letters for *all* specific epithets. Such a practice is followed in the rules of nomenclature governing zoological and entomological names, in the fifth edition of Bergey's "Manual of Determinative Bacteriology," and in the writings of some botanists. From this it may be predicted that in time the use of small letters for specific epithets, regardless of their derivation, will become universal.

10. The application of names of taxonomic groups is determined by means of nomenclatural types, or originals. Specimens used as a basis for specific names are type specimens, species used as a basis for generic names are type species, etc., into the higher categories.

11. *Nomina conservanda* (mostly generic names) have been established, and others may be added if authorized. These are declared valid, usually because of long-established use, even though in violation of one or more of the rules—most often that of priority.

12. When two groups are united because their members seem too much alike to justify separate grouping, the older group name is retained as the name of the united group.

13. When it is found desirable to divide a group because of the dissimilarity of its members, the group that contains the type on which the original group was based must retain the original name.

EFFECTS OF RULES OF NOMENCLATURE

While some botanists have dissented from certain of the International Rules, their use has been on the whole quite general and has resulted in bringing much order out of the confusion that existed before the adoption of the Paris Code. The few differences in practice that exist now are insignificant compared with those of a century ago.

In one respect the application of the rules has been a source of some annoyance. Botanists have been called upon to abandon plant names that they had supposed to be correct, but which, by the strict application of the rules, were nonvalid synonyms. Some of these were in very general use, but the finding of an older name for the same group in some obscure publication established the priority and consequent validity of an unfamiliar name. Well-chosen *nomina conservanda* seem justified as a remedy for this difficulty. Fortunately, the writers of manuals have been generally favorable to unification, although they have differed somewhat in certain details of application of the rules, particularly in the code to be followed.

CHAPTER X

PRINCIPLES OF TAXONOMY

In Chap. I the reasons for making a knowledge of evolution the basis of a working system of taxonomy were shown. Many principles have been developed to aid in applying this knowledge to the building up of taxonomic systems in both the plant and the animal kingdoms. The tracing of the progress of evolution and the application of it to the classification of existing plants and animals have been a challenge to the minds of some of the greatest scientific men for many years, and the work is far from finished.

DIFFICULTIES IN CLASSIFICATION

The classification of some hundreds of thousands of different kinds of plants is an enterprise of great magnitude and great difficulty. Even if we were content with an artificial classification that merely placed together plants and groups that resemble each other, much work would be required; but when we aspire to make a classification that will show all genetic relationships, the difficulties encountered are much greater and sometimes almost insurmountable.

Our greatest problem in plant taxomony is this: There are now many thousands of living species the relationships of which we wish to establish through genetic lines; but the memory and the records of man are so short that they do not show *direct* evidence of ancestry, and we have to rely on our own reasoning power to construct the genetic lines leading from the distant past to these existing species. The evidence we have consists of scattered fossils, the relationships of which are based on human judgment; morphological similarities that are open to varied interpretation; and our own evaluation of all this indirect evidence. Figure 92 shows the magnitude of the problem and offers, in part, a solution of it.

It seems certain that the first form of life must have been very simple—undifferentiated protoplasm much simpler than a one-celled green alga and capable of living and reproducing itself in an

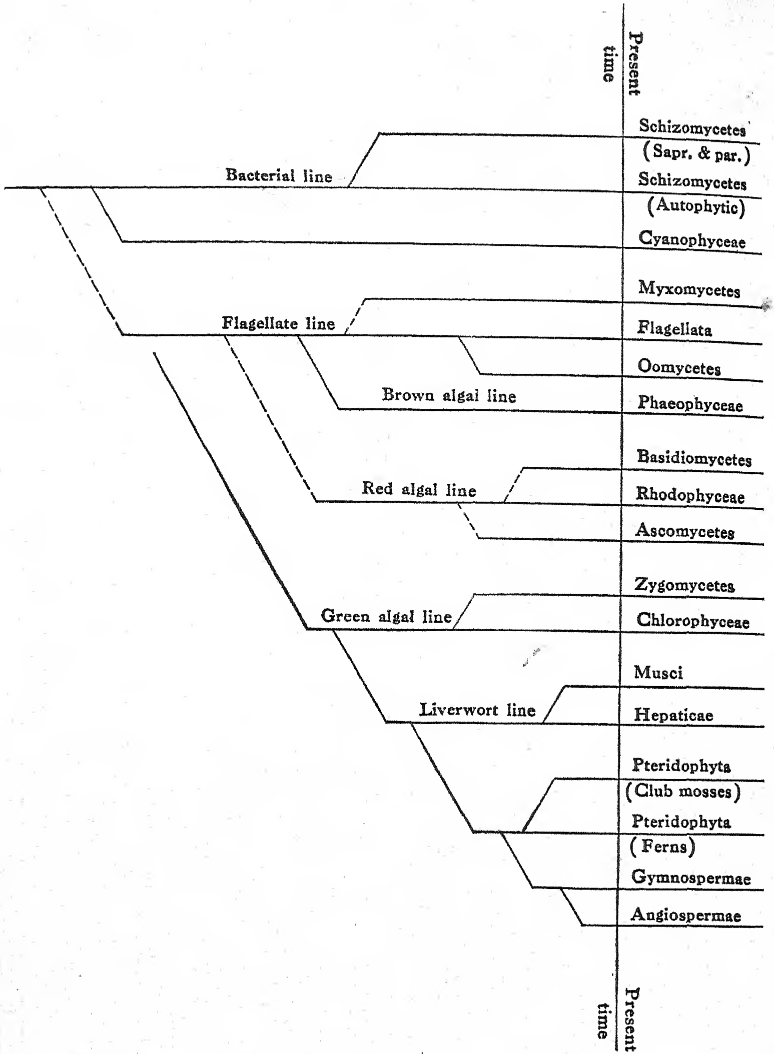


FIG. 92.—Suggestive relationships that may exist between groups of plants, past and present. Solid lines are based on stronger evidence than broken lines. (*From "Plant Life," D. Van Nostrand Company,* 1942.)

inorganic environment. From it the entire organic world seems to have evolved, but discovery of the steps in the process challenges the best efforts of the human mind.

Our efforts at plant classification have met with two practical difficulties: (1) the magnitude of the problem because of the num-

ber of species, and (2) the difficulties brought about by loss of ancestral forms.

Difficulties Due to Scope of Subject.—The pioneers in any subject make some mistakes, and early systematists were no exceptions. The magnitude of the work was so great that, with no organization among themselves and no governing standards, they labored at a great disadvantage.

The Logical Procedure.—If all the taxonomic work were to be done over again, the *logical* procedure would be to assign different parts to different workers who would confer from time to time in order to coordinate the units into a harmonious whole. Plant classification began, however, when science was in its infancy, and such an organization was not even dreamed of. Clearly the undertaking was too great for one man or one generation. None of the earliest botanists had a vision of the entire enterprise, and none could have carried it through if he had. Furthermore, the early work was purely voluntary and done mostly by men who carried a heavy load of other duties, or who had other interests and used botany as an avocation.

Work Done Piecemeal.—The natural procedure was followed. Each man studied the group of plants that happened to attract him, but many groups were neglected. Most of our best taxonomic work has resulted from group specialization. Naturally, those plants that were conspicuous or had an obvious economic significance received the most attention. When later botanists with a broader vision attempted to summarize the results and record them in more general systems of classification, they encountered several difficulties.

In the first place, many of the plants had been left unclassified, so they had to be placed in heterogeneous groups for further study or tentatively attached to groups where they did not belong; and in the second place, the better known groups had been classified by different methods, from different viewpoints, and by use of different characters. Some groups were so poorly constructed that they had to be entirely rebuilt, others were more or less modified, and still others were used in an imperfect form. The result is our present system of classification, good in spots but weak in others and not well coordinated.

Restrictions of Travel.—There is a good deal of variation in the floras of different countries. Botanists have never been able to

travel enough to compare all these different floras, and this difficulty was far greater in the early days than now. As a result, classifications have been made up on too limited evidence. Herbaria with representative specimens from different countries and habitats have improved the situation to some extent, but most herbaria are very fragmentary.

Limited Publication.—The next best thing to seeing plants is seeing pictures of them or reading and hearing about them. Some of our classification was made when botanical journals were unknown, and the meager writings in one language were little read by those speaking another. Many species that had been discovered and named were rediscovered and given other names by those unaware of the previous work.

The whole effect of the lack of intercourse and travel was to burden the tentative schemes of classification with duplicate names, synonyms, faulty descriptions, and a confusion of tongues.

Difficulties Inherent in the Subject Matter.—The desire for a classification was felt before the machinery was ready for making one. When we began to classify plants, we had no intimation of evolutionary origin, little knowledge of physiology or morphology, and no microscopes for aiding the eye in a study of tiny plants and the detailed structure of larger ones.

Pre-evolutionary Classification.—Prior to the work of Darwin, the viewpoints of classification were quite different from those that prevail today. Then there were two methods more or less used. One was to group plants according to economic uses, and the other to group them according to gross similarities in appearance. No attempt was made to work out phylogenetic relationships, for none were known to exist. Attention was given to the description of species, for each species was assumed to have been created separately; hence relationships of individuals within each species were recognized, and to some extent species were grouped into genera. Some even spoke of "natural affinities"— an expression of rather uncertain meaning.

Some quite elaborate systems of classification had been proposed before the doctrine of evolution was set forth. These systems, lacking the phylogenetic viewpoint, were more or less artificial, but it reflects credit upon morphology as an index to phylogeny that the classifications of de Jussieu, de Candolle, and Endlicher (see Chap. XI) had much in common with those of

today. Doubtless these could have been improved by further morphological study even without a knowledge of evolution.

The realization of the evolutionary origin of species has necessitated considerable readjustment of the older systems but not a complete revolution. Chiefly it has served as a guide in the reclassification of the more difficult parts of the plant kingdom where purely morphological characters had not been fully comprehended and interpreted. It has given a wholly new significance to comparative morphology.

Late Invention of the Microscope.—Had the microscope been in general use throughout the development of botanical science, the lower plants would not have been so long neglected. Most of the older classifications either ignored these smaller forms entirely or threw them into chaotic, unsorted groups. Lack of the microscope also delayed the discovery of complex life histories that have been found so significant in the fungi and even in such large plants as ferns and angiosperms.

Loss of Ancestral Forms.—It is not too much to say that "missing links" represent the rule rather than the exception in all studies of the phylogeny of plants and animals. We do not even know how many instances of algal degeneration occurred to make our present-day fungi, or the transitional forms between the green algae and the angiosperms. Paleobotany has done much, to be sure, but it is incomplete, with many gaps, and the chronological sequence is only approximate. If we had a record of all ancestral forms, it would solve most of the difficulties of phylogenetic taxonomy.

Degeneracy resulting in simplification is sometimes hard to distinguish from primitive simplicity. This fact has been troublesome in placing the bacteria, the yeasts, the Fungi Imperfecti, and even some of the flowering plants, *e.g.*, the grasses, and some deciduous trees (see page 205).

A Rigid System for a Flexible Subject.—The English botanist, John Ray, at the beginning of the eighteenth century, anticipated the feelings of many later botanists when he said, "Nature refuses to be forced into the fetters of a precise system." Notwithstanding this dictum, we make our definite groups and try to fit plants into them. As yet, we see no other way. The chief difficulty comes from intergrading characters. As shown later in this chapter, most of the major characters are not intergrading. If

they were as troublesome in this respect as certain minor characters, it is doubtful if our present system of taxonomy would be workable. Most of the controversies of modern taxonomists are due to four causes: (1) differences of opinion as to which forms of organs and structures are primitive and which are more advanced; (2) differences of opinion as to the relative value of characters for purposes of classification; (3) intergrading characters; and (4) unwillingness to sacrifice mechanical convenience to phylogenetic principles.

Of the difficulties presented here all can be overcome but two: the loss of ancestral types and the making of hard and fast categories where characters are intergrading. Paleobotanical studies will help to relieve the former difficulty and ecological studies the latter, for some of the gradations, not all, are merely the effects of environment.

BASES OF TAXONOMY

Probably the most interesting scientific aspect of systematic botany is the determination of phylogenetic relationships. They present a record of the products of evolution modified by geological and climatological agencies. Phylogeny is, however, a most difficult subject, for many of the evidences have been effaced. If we had a written record of all the forms of life on the earth from the beginning to the present time, the phylogeny of any group could be derived by sufficient study, but in the absence of such a record we have to resort to more or less indirect evidence, which will be discussed later.

Phylogenetic Evidences.—In all studies of phylogeny the origin of groups and individuals by evolution is assumed as axiomatic, for if there had been an independent creation of each species, there would have been no relationships between them. Once we accept this doctrine, then, our problem is to trace the relationship of existing individuals and groups back through their ancestry, most of which has long since disappeared leaving only a few scattered fossils and other traces.

Until recently our knowledge of phylogeny in plants was based chiefly on three lines of research, comparative morphology, anatomy, and paleobotany. These are now being supplemented by a number of others, including ecology, plant geography, cytology,

genetics, and serum diagnosis, which are discussed later in this chapter (page 259).

All modern tendencies are toward making phylogeny the underlying principle of taxonomy, but phylogeny is not in itself a tangible thing that appeals to the senses. We must, therefore, have usable criteria by which to determine phylogenetic relationships.

Morphology as an Indicator of Relationships.—The close similarity of certain plants to each other appealed to the early botanists long before the concept of evolution was developed. They were, therefore, fairly well prepared for this new idea and diligently set about applying their knowledge of morphology to its interpretation. A few laws gradually took form to aid them, principally (1) that life has usually advanced from the simple to the complex (progressive development) but has sometimes been simplified by degeneration or loss of parts (regressive development); (2) that the simpler forms of life now existing are more like their ancestors than the complex ones (though not exactly the same); (3) Haeckel's law of recapitulation, that ontogeny is a brief repetition of phylogeny; (4) Dolle's law of irreversibility in evolution, that a product of evolution never goes back to an ancestral condition; and (5) that homologous rather than analogous structures indicate relationship. To these laws have recently been added the "morphological indicators of phylogeny" set forth on pages 276 to 280.

Both in animals and in plants morphology is the most widely used instrument of classification. This was true before the time of Darwin and it is true today, though we now use it more intelligently in the light of our knowledge of evolution. An indicator to be useful must be fairly easy of application and reasonably accurate. Genetic relationships usually express themselves through similarities and differences in form and structure. These different characters are in themselves numerous, and considered collectively they present almost endless combinations. Also, morphological differences appeal to the eye, usually on brief inspection, and offer a rapid means of classification. Practically all herbaria, all systems of taxonomy, and all botanical manuals are based almost entirely on comparative morphology and anatomy; and even though the newer experimental methods of cytology, genetics, and ecology may throw light on the mechanism of evolution (see page 19) and on phylogeny in the lower

categories—genera, species, subspecies, etc. (see page 262)—they cannot soon, if ever, entirely replace the older taxonomy based on morphology and anatomy. That the experimental method will amplify the morphological, help to explain it, and correct some of its errors there can be no doubt. Morphology does not suffice, however, in certain groups of lower plants, particularly those pathogens in which similar-looking fungi or bacteria cause different diseases, thus indicating a difference in their species. It is a somewhat unsatisfactory indicator in the Fungi Imperfecti, where only asexual reproduction remains in plants once possessed of sexual stages of various kinds. For example, *Fusarium* is a form genus based on the appearance of the conidia, but conidia of similar appearance are known in different genera of well-known Ascomycetes.

Difficulties in Applying Morphological Indicators.—Throughout the Christian Era up to the twentieth century there was an accumulation of morphological data far beyond the ability of botanists to interpret. Progress was made to the point of placing many of our plants in more or less well-defined species, genera, and families. Some crude attempts also were made at classes and divisions, resulting in such groups as thallophytes, fungi, and seed plants, quite different from the carefully constructed phyla that some have since proposed. For the most part, classification prior to the twentieth century took this form: that certain genera were believed to constitute a certain family (often called an order), certain families to constitute a certain class, etc., but how the smaller groups should be arranged within the larger was undetermined.

One of the difficulties in using the accumulated mass of morphological data for phylogenetic purposes was lack of knowledge of major and minor characters (see page 264), and there is still some disagreement in this field. For example, the distinction between woody and herbaceous plants was given great prominence up to the middle of the eighteenth century, was then relegated to a minor position, but in 1926 was revived again by J. Hutchinson[1] in a more scientific form based on anatomy and histology as well as on external form and general texture. Its relative importance is again a matter of controversy.

[1] "The Families of Flowering Plants," Macmillan & Company, Ltd., London, 1926.

Another difficulty lay in determining which of two forms of an organ was the more primitive and which the more advanced; *e.g.*, separate versus united petals, persistent versus deciduous leaves, and one versus two cotyledons. On this subject a summary of our present usage is given on pages 276 to 280.

Internal Anatomy as an Indicator of Relationship.—The difference in stem structure between monocotyledons and dicotyledons has long been recognized, the former having scattered fibrovascular bundles and the latter having bundles arranged in a cylinder enclosed by a cortex and surrounding a pith. Later, differences were noted in the leaf traces—branch bundles running out into the leaf petioles and floral parts—and, in the dicotyledons especially, differences were observed in the details of secondary thickening of stems by the addition of more phloem and xylem. The fact that some trees have heart- and sapwood while in others there is no such distinction has been known for centuries.

Histological differences in the xylem have also been observed, xylem vessels (tracheae) in the angiosperms replacing the more primitive tracheids of the gymnosperms and tyloses being formed in the old vessels of some woody species but not others. Recently, finer distinctions in the character of the wood, especially the size and walls of the xylem cells, have been studied to the point where keys for specific identification have been made on wood structure alone,[1] with no reference to external morphology. Evidence dealing with the identification of woods by microscopical examination is now accepted in criminal cases. Anatomy and histology are reliable indicators of relationship where they are applicable, but they are more time-consuming than morphological observations, and there are many species of herbaceous plants in which they have not received special study.

Physiology as an Indicator of Relationship.—It is a well-known fact that groups of plants differ more or less in their physiology. These differences may be either qualitative or quantitative and may or may not be accompanied by morphological differences. Physiology, however, is a cumbersome basis for classification. If we had to perform a series of physiological experiments to tell one species from another, progress would be slow. It would be very tedious, for example, to establish families on the basis of the com-

[1] See Samuel J. Record, "Timbers of North America," John Wiley & Sons, Inc., 1934.

pounds of nitrogen in the soil that are best suited to their use as food materials. Furthermore, the usual physiological processes, especially among chlorophyll-bearing plants, are not established as dependable criteria of species. It is doubtful whether families constructed on a basis of nitrogenous food requirements would show phylogenetic relationship. In many cases they are too unstable, for in response to changes in environment, heat, light, food, moisture, etc., plants show changes in physiology much more readily than in morphology. For this reason physiological differences are little used except to supplement morphological ones, as in the lower groups just mentioned where the latter alone are not sufficient. It seems unwise, however, to rule out physiology entirely, as some systematists have been inclined to do, especially as serum diagnosis (see page 247) is really an interpretation of a physiological reaction. Such an attitude has the effect of discarding a tool that is sometimes useful, especially in classifying bacteria and fungi.

Paleobotany.—Morphology of existing forms of plant life gives incomplete evidence of phylogeny because of the many ancestral forms and connecting links that have long since disappeared. Some of these have been preserved as deposits and recognizable fossils.

There is evidence that the first life began in the sea, which at that time covered nearly all the land and was not so salty as at present. Probably the first forms were so delicate and so scattered that they left no remains that can now be detected. Later, the more abundant and substantial forms left deposits of graphite and carbonates, but the cellular structure was quite obliterated. Still later, plants and animals with more solid portions, skeletons, heavy cell walls, etc., dying in localities favorable to their preservation, became covered with earth, and a few of them have been recovered as fossils. Doubtless many more are still hidden.

Some of these fossils are merely impressions of the plant part on plastic material that later hardened into rock, while the plant itself quite disappeared. Others consist of plant parts replaced bit by bit with mineral. The slow molecular replacement has produced the best fossils, for in them even the cellular structure is often preserved, sometimes quite faithfully.

The great value of these fossils lies in their chronological history of ancestral forms, "missing links" in evolution, and in their

record of evolutionary morphology—the sequence in the development of organs. Most fossils represent extinct species that are, nevertheless, named and classified. Others correspond to species that still exist practically unchanged. In numerous cases fossil records have confirmed or corrected opinions based on the morphology of living plants as to the relative antiquity of existing groups, thus showing the trend of evolution. Through the researches of historical geology the strata of the earth's crust have been classified, the method of their formation determined, and with some approximation their ages have been estimated (see frontispiece). Through a combined study of geology and paleontology the climates on the earth at the different periods and the effects of these climates on the forms of life existing at those times (see page 12) are known to some extent. It is probable that the different phyla of plants and animals originated during profound and disastrous climatic and geological changes that exterminated many species. Vicissitude begets hardy races.

Unfortunately, the paleontological records are very fragmentary. While they have yielded much of value and have modified and supplemented somewhat our interpretations of present-day morphology, they have left much unsaid. The softer plants, such as green algae and liverworts, usually failed to leave a recognizable impression, and even most woody plants decayed and disappeared entirely except under the most favorable conditions for preservation, such as burial by mud. We do not even have a record of the evolution of flowers from the ancestral sporophylls; for although both sporophylls and flowers have been fossilized, transitional forms are lacking. Much is hoped for in the future, for in all likelihood man will continue to find and interpret fossils for many centuries.

Serum Diagnosis.—An important physiological or chemical indicator developed to show phylogenetic relationships is the serum diagnosis of Carl Mez, of the University of Königsberg, and his associates and students. When it is desired to determine the relationship of one kind of plant to another, the proteins of the two are compared, those with proteins most similar being interpreted as most closely related. To this end a protein extract is made from one kind of plant and injected into the body of a rabbit. After waiting a suitable time for the rabbit's body to react to the protein, its blood is drawn and the serum is mixed

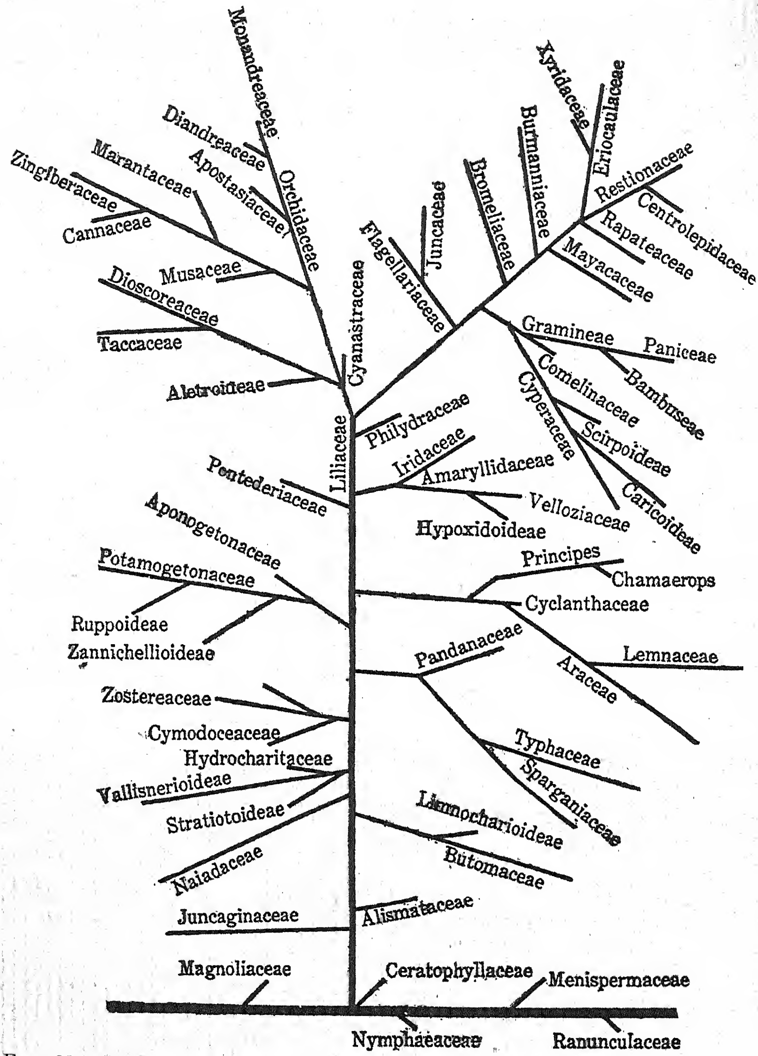


Fig. 93.—Phylogenetic arrangement of the monocotyledons as indicated by serum diagnosis. (*Redrawn after Ankermann.*)

with the protein extract of the second kind of plant. If a precipitate forms, relationship is indicated. If such a precipitate forms when a high dilution of the serum is used, the relationship is considered closer than if it forms only with serum that is less diluted. A remarkable phylogenetic tree has been constructed on the

results of these reactions, one branch of which is shown in Fig. 93. The relationships thus indicated generally, but not always, correspond with morphological conclusions, and it is noteworthy that the phylogenetic lines form a branching, not a reticulate, system and thus conform to rule 1 of the principles on page 277. The Mez, or Königsberg, serum diagnosis must be looked upon as a valuable supplement to morphological studies for the determination of relationship, although the work needs much verification and has not always been found reliable.

PLAN OF TAXONOMY

Taxonomy must be looked upon as an attempt to determine the relationship of plants by studying their similarities and differences and thus to build up a system of classification. The mind of man cannot comprehend each separate individual of the millions of plants on the earth; hence it is necessary to think of them in groups, generalizing their characters in so far as it is safe to do so. This necessity and the tendency of the scientific worker to be orderly have led us into many of our taxonomic problems.

As a result of centuries of study and discussion, botanists and zoologists have learned much that is essential to logical classification, and the two branches of biological science use essentially the same plan. Probably the work of Linnaeus, who named and classified both plants and animals, contributed something to this uniformity. There is now a pretty general agreement on the main principles and a fair uniformity of practice except in certain details, where some difference still exists. Each kingdom is subdivided into great groups and these into smaller groups until the species is reached, the species being a collection of individuals that are *essentially* alike. In some species even lower categories are recognized.

CATEGORIES USED IN TAXONOMY

The term "category" is used to designate a group of any *definite* rank, large or small, into which plants or animals are classified. Classes, genera, species, families, etc., are examples.

Categories must be made to fit plants, as plants cannot be changed to fit categories. As a forerunner to the categories we now have, certain group entities were noted many years ago. Some of these were small groups; others were large, including

these small groups and additional ones. Thus the flowering plants were thought of as a very large group including legumes, mints, umbellifers, daisies, etc., and legumes were known to include various kinds of clovers, vetches, peas, etc. Centuries of study yielded a mass of information about groups of plants, and we have attempted to make usage more uniform by adopting the system of categories given below. Always we must think of them as man-made attempts to simplify and express a complex, unstandardized, and constantly changing mass of living things.

For convenience and uniformity a rather definite series of categories for the plant kingdom has been adopted. The regular categories, ranging from the largest to the smallest, are as follows: kingdom, division, class, order, family, tribe, genus, and species. These terms have each been given as definite a meaning as possible, and they must not be used loosely or interchangeably.

Most categorical names have, for convenience, definite endings. The names of all groups larger than genera are given the plural form. The names of orders usually end in -ales, those of families in -aceae, and those of tribes in -eae. The following is an example showing the sequence of categories to which the rose belongs and the proper endings.

Division Spermatophyta
  Class Angiospermae
    Order Rosales
      Family Rosaceae
        Tribe Roseae
          Genus Rosa
            Species rugosa

In special cases the qualifying prefix "sub" may be added to any of these, as subclass, subgenus, etc. This practice is for convenience where the group is a large one containing many members and especially where these members fall into two or more natural groups. For example, the great class Angiospermae is commonly divided into two subclasses, monocotyledons and dicotyledons. Some botanists, however, carry this practice too far and make suborders, subfamilies, or subgenera where the evidence to justify it is trivial or debatable, and some create confusion by using the term "subfamily" for groups that others call tribes.

There is no uniformity in size among the categories. One

genus may contain dozens of species and another only one or two. Except to satisfy a desire for uniformity of procedure, several categories might have been omitted in the smaller groups. For example, the family Adoxaceae has only one species, *Adoxa Moschatellina*. If all families had been as small, or even contained but a half-dozen genera, probably families and tribes would never have been devised, and orders would have been divided directly into genera, or there might have been families with no orders or tribes. In actual practice, tribal names are not often used except in the larger families, and the ordinal names of the higher plants are omitted from many of the manuals of this country.

What Constitutes a Species.—To give categories a definite meaning there must be a starting point. To say merely that an order is a collection of related families, each of which is a collection of related tribes or of genera, does not give a full comprehension of the meaning of these terms. Most authorities look upon the species as the unit of classification and then build the higher categories upon this conception. Others prefer to consider the genus the unit. As most species are made up of individuals so nearly alike that no need has been felt for a finer subdivision, it best suits the majority of botanists to use the species as the classification unit, subdividing it into subspecies, varieties, races, etc., only in those species where such a procedure serves a useful purpose.

One of the most troublesome problems in taxonomy is to arrive at a definition of a species upon which all can agree. The question of defining a species is so perplexing that it has been made the subject of several research papers and at least one symposium. There are two older conceptions, each having a considerable following. Certain botanists, notably de Candolle, Linnaeus, and Gray, constructed their species along bold and clear-cut lines, each species being separated from its relatives by distinct and easily differentiated morphological characters. Trivial differences were ignored, particularly those that were only matters of the degree in which minor characters were shown. In some of Linnaeus' species the different individuals showed considerable minor variation. In others they were essentially alike. Linnaeus' species lacked uniformity of character, however, because some of his work was compilation based on plants he had never

studied. This broad method of species making reached its greatest perfection in the work of Asa Gray. By his usage the number of species was kept relatively low, and identification of plants to the species was comparatively easy. The expression "Linnaean species" has come into accepted use for these bold, easily distinguished groups with clear-cut characters, and it will be used here, although "Grayan species" may be a more accurate term. Some taxonomists follow the arbitrary rule of insisting that at least two morphological differences be required to separate one species from another.

The other conception was that of "elementary species" or "primary species." It is practically true that no two individuals are *exactly* alike. In an elementary species the individuals must be as nearly alike as though they had the same pure line parentage. This idea involves the necessity of making separate species of all plants showing any constant differences whatsoever, no matter how trivial or minute; and in some species so made the differences are not even constant, single specimens of unknown lineage, some of them merely ecological modifications, having been given new specific names. It will be readily perceived that this plan, if extensively carried out, would vastly increase the number of species to be dealt with. *Draba verna* L. is cited as an example of a species of the Linnaean and Grayan kind that could be divided into more than 100 elementary species. Where intergrading characters are found there may be almost as many elementary species as individuals. Such a system becomes burdensome and detracts from the usefulness of taxonomy. Furthermore, where "species splitting" has been carried to such extremes, as in the genus *Crataegus*, the specific distinctions are so hard to follow that only the specialist in that group can carry on the identification.

One taking an impartial view of the species question is forced to this conclusion: that for most of the plant kingdom the bold Linnaean type of species is simpler than the finely divided elementary species and serves every essential purpose; but in certain groups it may be necessary to make finer distinctions for research reference, though even there the majority of botanists may not need to do so for their more general work. The natural answer is the assembling of the individuals into relatively few, large, clear-cut species and, where necessary, having additional

fine distinctions to be used only by those who have special need for them. Various terms have been used to designate these finer divisions, such as subspecies, varieties, races, types, and forms. To be sure, this introduces the trinomial nomenclature; but if this is cumbersome, it has the advantage of showing relationship, for the specific name connects the related subspecies to each other. Species making as done in the past has been based on simple inspection of individual plants. Geneticists and ecologists are working on a more exact, experimental method, which, however, requires extensive research on each species (see page 262).

The Newer Species Concept.—The conception of a taxonomic species given above is the classical one that has been in use for centuries, starting even before the time of Linnaeus. There is a newer species concept, based on genetics, cytology, and ecology in addition to the conventional morphology and geographical distribution, that has a more scientific basis. It aims to be a more objective concept—to have a broader foundation of facts and hence to enable one more clearly to visualize what natural units have evolved. It will be explained here, even though it has been applied to relatively few groups of plants as yet, and its universal application must await an immense amount of research. It merits our attention because the results of its use up to the present time suggest that it will prove of wide application, and its methods must be taken into increasing consideration by all taxonomists.

This newer conception is based on experiments that indicate that natural systematic units are kept apart, and successful crossing is prevented by barriers of various sorts and degrees. The barriers that are found separating different species within the genus can be studied experimentally, whereas those more profound ones that separate genera and the higher groups do not lend themselves to such analysis.

Two kinds of barriers are found: internal (hereditary) and external (environmental). If there were no barrier to block free intercrossing and migration, all the members of one genus would belong to a single species. This is the case in a few genera. In most instances, however, hereditary and environmental barriers are operative to separate both species and lower units. The hereditary barriers to successful crossing may involve the number or structure of the chromosomes, or they may be primarily gene-

controlled. Differences in chromosome number in plants that reproduce sexually almost always indicate that different species are involved, according to this concept, because this is a formidable barrier to successful hybridization. Rearrangements in chromosome structure may likewise render forms wholly or partly intersterile, the resulting offspring, if such are formed, being victims of their own inherent weakness or of a hostile environment.

The various genetic barriers often take the form of incompatibilities or inherited weaknesses that tend to eliminate the hybrid offspring and maintain the pure units. Both morphological characters and physiological functions, such as growth and flowering, are affected. The environmental barriers are either geographic or ecologic.

Under this concept species of the same genus are separated primarily by genetic barriers. The species may be unable to hybridize at all if their genetic isolation is complete. If it is but partial, they may produce hybrids which are partially sterile or which produce a weakened second generation not as well fitted to survive in nature as the original parent species.

A few instances have been discovered in which plants are found to be entirely intersterile, and it is impossible to link them through crossings with an intermediary, yet they cannot be distinguished morphologically. Biologically, these are distinct species. However, in these rare cases in which genetic differentiation has preceded the morphologic, good taxonomic practice dictates that the forms be retained within the same taxonomic species.

The experimentalists are finding that species that are unable to cross may or may not occupy the same environment, while those that can cross grow largely in different areas. At those places where their ranges of distribution overlap, hybrids between them are also to be expected. If species that can cross, even though with only partial success, occupied the same range, they would soon lose their identities through hybridization.

The subdivisions of species, such as the subspecies, variety, race, etc., are able to interbreed freely when the opportunity offers, but they are separated by environmental isolation. This isolation seems to be almost always geographical, and it is thought to be maintained by natural selection, *i.e.*, adaptibility to the environment or the lack of it. Correlated with the environ-

mental isolation, there may be characteristic differences in appearance.

This newer species concept attempts first to work out the stages of evolutionary differentiation found in nature and then to assign ranks to the groups recognized. Some transitional stages are found that are, for instance, neither species nor subspecies, thus reaffirming the idea that evolution is a continuous process. Few students are in a position to follow the exhaustive experimental program called for to apply this concept with complete assurance. Nevertheless, the work to date stresses the significance of geographic and ecologic distribution and of chromosome numbers to taxonomy—data not out of reach to most workers.

Of course, it is very difficult, if not impossible, to apply the new definitions, before actual experimental work is done, to the thousands of species of plants that have long been recognized. Fortunately, however, the species of the experimentalist is frequently identical with that which has been carefully worked out on the basis of comparative morphology and distribution. This means that the new methods will not overturn our existing classification but will amplify, stabilize, and clarify the position of the systematic units and help to explain how new species arise.

Other Plant Groups.—Generic distinctions and those of higher categories give much less trouble than the lower ones. To be sure, there is some difference of opinion as to what categorical rating should be given to certain groups, *e.g.*, whether they should be considered orders or families, families or tribes, genera or subgenera. In fact, several families have been divided by certain authorities who would call the legumes and the composites orders rather than families. These differences are not disturbing, however. Because of the absence of gradations in characters used in class, order, and family distinctions there is usually little difficulty in placing a plant correctly in these large groups, and even generic classification is seldom troublesome. More difficult is the problem of determining whether certain large groups, *e.g.*, pteridophytes, dicotyledons, monocotyledons, umbellifers, and composites are monophyletic or polyphyletic. If they are polyphyletic, the logical procedure would be to divide them.

Where a *general* term is needed for any collection of plants that may or may not have phylogenetic relationship and therefore may or may not have a categorical rating, often having only a similar-

ity that does not indicate true relationship, the word "group" is used. Thus, all deciduous trees form a group, or all aquatic plants, or all insect-catching plants; but the word can also be applied to all roses, all mustards, or all grasses, members of which do show actual relationship.

The phylum in zoology is a definite group consisting of related classes. In botany the phylum is not generally recognized as a regular category. It is, however, a most valuable group, ranking usually between the class and the division. The phylum is constructed on logical phylogenetic lines. The division, on the other hand, may be a heterogeneous *polyphyletic* collection. This criticism applies especially to the division Thallophyta, which is composed of bacteria, slime molds, and several unrelated classes of algae and fungi.

SUBSPECIFIC CATEGORIES

In a general way the term "subspecific categories" refers to all those that are used to subdivide the species into still smaller groups. More definitely, the *subspecies* is a category in itself, ranking between the species and those still lower. Most species are not thus subdivided, since the species is the unit of classification, but a few exceptions are made by some botanists. There are several kinds of subspecific categories.

Varieties.—The variety is the subspecific category that is sometimes used in the classification of wild plants. Linnaeus, the great exponent of binomial nomenclature, gave more than 200 varietal names in his "Species Plantarum," thus establishing trinomials. Varietal names can still be found in some botanical manuals, *e.g.*, in Gray's "New Manual of Botany," seventh edition, and in Coulter and Nelson's "New Manual of Botany." An example is *Salix glaucops* var. *glabrescens* Anders. Usually the varietal distinction is based on a single minor character such as epidermal hairs or size, the plant otherwise being like the species of which it is called a variety. Britton and Brown, in their "Illustrated Flora of the Northern States and Canada," entirely eliminated varietal names, since they are really a form of trinomial nomenclature. However, the desirability of retaining them in some cases cannot be denied.

If it seems advisable, varietal names based on morphology alone can be avoided, or, once established, they can be eliminated

in either of two ways. The trivial character on which they are based can be ignored and only the generic name and the specific epithet used, or, if the character seems of sufficient importance, the varietal name can be raised to the rank of species. Thus *Salix glaucops glabrescens* can become simply *S. glaucops* or *S. glabrescens*. On the other hand, a specific epithet may be reduced to the rank of a variety. A sand plum was named *Prunus Watsoni* by Sargent and changed to *Prunus angustifolia* var. *Watsoni* by Waugh. Morphological observations alone, unsupported by experimental evidence, may be insufficient to determine whether a group should be rated as a species, a subspecies, or a variety. Certainly these lower categories—subspecies, varieties, races, forms, etc.—are not as definite categories as genera, species, and higher categories, and taxonomic authorities[1] differ in their usage.

There is at present considerable controversy as to whether the older term "variety," used by Linnaeus, Gray, and others, should be replaced by "subspecies." Some hold that the word "variety" has so many different meanings that it should be used in botany only for agricultural and horticultural productions. Others claim that it has served well in the past for subdivisions of wild species and that this usage should be continued.

Varieties or species based on fine distinctions of a somewhat permanent character must not be confused with ecological or environmental modifications of a temporary nature. It is well known that closely related individuals growing in different habitats may vary considerably, so much, indeed, that they are sometimes called different species. It would be desirable, though sometimes impracticable, to have representatives of related species grown side by side for comparison. Such tests have shown that some species are practically identical if grown in the same environment, and research along these lines could be used to eliminate many superfluous specific names from our manuals. There would also be involved, in some cases, the practice of including in the specific description qualifying statements concerning the effect of environment and corresponding records showing the habitat of the specimen in question. The work now being done in

[1] See Robert T. Clausen, On the Use of the Terms "Subspecies" and "Variety," *Rhodora*, **43**: 157–167, 1941; also, F. Raymond Fosberg, Subspecies and Variety, *Rhodora*, **44**: 153–156, 1942.

this field by ecologists will greatly strengthen our taxonomic systems. For further discussion of this topic see page 261.

Horticultural and Agricultural Varieties.—In most species of cultivated plants, different varieties are recognized. Examples are the Delicious variety of apple, the Golden Bantam variety of sweet corn, the Marquis variety of wheat, and the Spencer variety of sweetpea. Generally these varietal distinctions are based on qualities of economic importance, such as size, color, or flavor. Such varieties are generally the products of the practical plant breeder, but occasionally they are found by man rather than produced by him. The present tendency of some botanists is to avoid the term for wild plants and restrict it to cultivated ones.

Biological Races.—Among some parasitic fungi, notably the rusts and smuts, it has been found that a species is made up of races that are morphologically alike but differ in their ability to attack different host plants. *Puccinia graminis*, for example, includes dozens of such races. One of these can attack certain grains and grasses, while others can attack different hosts and perhaps some of these as well. The races are distinguished from each other through experiments carried out by inoculating with the spores of a strain of the fungus to be tested a large number of related hosts, differing in species or variety, and noting which ones are parasitized and which ones escape. Usually these biological races are numbered but not named.

Serological Types of Bacteria.—Pathogenic bacteria of certain species that cause human diseases have been divided into types on the basis of their behavior toward the blood serum of persons or animals injected with the bacteria or their products. In effect the serum diagnosis is a comparison of the proteins of one species with the proteins of other species, those with proteins most similar being interpreted as most closely related.

Ecological Modifications.—It has long been known, and recent studies have emphasized, that morphological differences may be a direct result of environmental conditions and are not heritable. In some cases the mistake has been made of giving new varietal or even new specific names to such plants. These variants of a temporary nature are not entitled to a taxonomic rating.

Strains.—The term "strain" applies to a line of plants from a *single source*. It is used for either higher or lower plants that are under cultivation. Thus each seed house or nursery may have

its own strain of Golden Bantam corn or Golden Wax bean; anyone can catch a strain of *Rhizopus nigricans* from the air, and bacteriologists isolate strains of *Bacillus subtilis* from the soil. Strains of the same species or variety are not necessarily unlike each other—quite frequently they are practically identical.

CONTRIBUTIONS OF OTHER BRANCHES OF BOTANY TO TAXONOMY

There is at the present time a considerable uniformity of opinion as to the relationships of the larger groups of plants, groups that we believe have been represented on the earth for many centuries.

There is every reason to suppose, however, that evolutionary processes are still going on. In all likelihood some species are still giving rise to newer ones, although others are, for the present at least, remaining constant. Such a situation has always characterized organic evolution. We do not expect new families or orders to come into existence suddenly, but new species are inevitable. It is natural, therefore, that research in this field should be concentrated on species and subspecies.

Keeping in mind the great goal of taxonomy in its effort to organize all plants and plant groups, past and present, along phylogenetic lines, and realizing the scarcity of records or *direct* evidence on which to base a complete phylogenetic system, systematists are using every branch of biology that offers any contributions to the solution of taxonomic problems. The most important of these are paleobotany, plant geography, cytology, genetics, and ecology. Some of the most effective work is done through a combination of two or more of these branches of biological science.

Paleobotany and Plant Geography.—Both of these subjects have been studied for a long time and have great interest in themselves. Recently, use is being made of them to work out the origin, history, and development of plant groups from the standpoint of plant relationships.

Often it has been possible to determine the locality and geological period at which the group originated, information that suggests its probable ancestors, and to trace its spread from the original source and its branching into smaller groups—genera, species, etc. Ecology here becomes a part of the picture in

determining and explaining the distribution of the species as they evolve. Much of modern research in taxonomy consists in studying limited groups, such as genera, from every angle, including historical development, and using the results obtained as the basis for a taxonomic monograph.

Many times plants practically identical in morphology but growing in different parts of the world have been given the same generic but different specific names, and some that have been given the same name when found in widely separated regions have been found to be different in their tolerance of ecological conditions when brought together and therefore probably deserve different names. This suggests that the physiology of a plant with respect to its adaptability to environment should be considered along with morphology in determining species.

Cytology and Genetics.—For many years cytology consisted merely of a study of the finer details of plant and animal structure, with emphasis on those of the nucleus. It has since been enlarged to include an interpretation of the behavior of the organs of the cell, especially in reproduction. Genetics makes use of the findings of cytology and other branches of biology, especially Mendel's work, to establish laws and principles governing evolution—the fundamental basis of taxonomy. This subject has been briefly discussed under "Mechanism of Evolution" on page 19.

All evolutionary change appears to be based on the behavior of the chromosomes and their included genes. These in turn are known to be affected by environmental conditions, such as extreme temperatures and X rays. The effects are initiated while the nuclei are dividing or uniting and cause changes in the offspring. The best known of these results, which some would class as abnormalities, are changes in the number and composition of the chromosomes—polyploidy, etc.—and changes in the genes themselves, about which little is yet known. Indeed, many of the variations and mutations that have been observed in plants will require much work for their explanation.

Cytology and genetics work together so closely that to carry on research in either field one should be well versed in both. These fields, with ecology, have become the strongest supplements to the older taxonomy based on comparative morphology and anatomy.

Ecology.—The subject of ecology is no longer restricted to observations on the effects of climatic and other environmental

conditions and noting the kinds of plants found associated with each other, but in conjunction with cytology and genetics it is offering deeper explanations than were previously available into the meaning of taxonomic relationships.

A simple type of ecological experiment is now becoming more widely employed on taxonomic problems to supplement the morphological observations. It consists of studying representatives of related groups, such as different races of the same subspecies, different subspecies of the same species, etc., when grown side by side in a uniform garden. The differences one observes in the wild state between related plants may be hereditary, or environmental, or, as is usually the case, a combination of both. When the plants are assembled in a uniform garden these hereditary differences will stand out, unconfused with modifications caused by unlike environments.

Another step is to study the same plants in different habitats. This may take the form of comparing the growth of individuals brought to regions differing strongly from each other in climate, or submitted to different local conditions in the same climate. The purpose of such experiments is to study the reactions of the individual and to compare the range of tolerance of related plants to a given series of conditions. Here the ecological aspect of the experiment merges with the genetic, because the range of tolerance of plants for different environments is genetically determined. Often perennials are employed that can be propagated vegetatively, so that parts of the same individual can be grown simultaneously under different conditions. In this way the heredity of the plants is the same, and the differences that develop between them will be due to modification by the environment only.

Transplantation experiments have shown that the morphology of the plant, while controlled by both heredity and environment, is less affected, except for size, by the environment than many botanists have assumed. What is more important, it has been learned that environmental conditions sort the natural units presented to them, such as species, subspecies, populations, etc., with a ruthless hand, completely eliminating many and forcing others into definite geographical patterns of distribution. For instance, some species are narrowly limited in their distribution to the only environment to which they are suited, as the redwood, *Sequoia* spp., while others such as the yarrow, *Achillea milli-*

folium, are adapted to many environments and have a wide distribution. Species of wide distribution are furthermore found to be composed of many races, each adapted to a different climatic region and usually distinguishable in appearance. These climatic races of widely distributed species are the basis of the experimentalist's subspecies.

The Experimental Method in Taxonomy.—For centuries the classification of plants was based on comparative morphology and anatomy alone, although it had been observed that the successful crossing of plants could be accomplished only between those that were closely related. Only during the present century has the significance of geographic distribution been generally appreciated. Through research work in genetics, cytology, ecology, and plant geography a newer experimental method of studying taxonomic problems is being developed that should prove to be a valuable supplement to the older one. This method is being developed simultaneously in several centers, notably in Scandinavia under the stimulation of the work of the Swedish botanist, Göte Turesson, in Great Britain, and in the United States by the Carnegie Institution of Washington and the Agricultural Experiment Stations. Related work is being done in zoology.

The experimentalist attempts to assemble in his gardens as many forms as possible of the group he is studying, using the herbarium as a source of reference to the forms that may be looked for in nature. Then he hybridizes these extensively. Some crosses are failures, others are successful, producing fully fertile hybrids, while still others produce partially or completely sterile hybrids. Cytological studies show some of the nuclear changes, especially in chromosome numbers. Gradually a picture of the genetic relationship of the forms is built up. All degrees of relationship are found, but in general the forms with closely similar morphology, which the observer would presuppose to belong to the same species, are found to be highly interfertile. Likewise, plants of unlike morphology ordinarily prove to be genetically unlike and incompatible. However, expectations based on appearance do not always accurately forecast experimental results.

From a consideration of the combined evidence offered by the morphology, distribution, genetics, cytology, ecology, and reactions to transplanting, the experimentalist is able to arrange

his plants in units of different orders of magnitude. On the basis of their genetic affinities he determines which groups are to be treated as species, which as subspecies, etc. From the herbarium and the literature he determines what names can best be applied to these units. Since the resulting classification is based upon various kinds of facts, it will more closely approximate the aim of taxonomy to present a true picture of phylogenetic relationships than would a classification based upon only one or two kinds of facts.

The units first worked out by such methods were given genetic-ecologic terms by Turesson.[1] Originally, no attempt was made to correlate these terms with existing taxonomic terminology; but as experimental evidence accumulates, it becomes possible to compare the names of natural units determined by experiment with those commonly employed in taxonomy. Since the two systems are based upon different characteristics, however, an *exact* statement of equivalents is quite impossible.

The following terms, the first three of which were proposed by Turesson, are correctly applied only to groups whose rank has been determined by experiment. They are presented here because they are entering taxonomic literature to an increasing extent as the experimental methods are becoming more widespread.

A *cenospecies* is a group of plants that can be linked together by at least slightly fertile hybrids. Considerable genetic incompatibility and much morphological dissimilarity may exist among its members. One or more ecospecies are included in a cenospecies, which is frequently the equivalent of a taxonomic genus or subgenus.

An *ecospecies* is a group of plants whose members are interfertile among themselves but are prevented from free intercrossing with other groups by either complete or partial genetic barriers. When the ecospecies is morphologically distinguishable from others, it corresponds to the taxonomic species.

An *ecotype* is a group of plants adapted to a particular environment but capable of producing fully fertile hybrids with other ecotypes, if any exist, of the same ecospecies. Its identity is maintained by ecological isolation operating with natural selec-

[1] Turesson, Göte, The Genotypical Response of the Plant Species to the Habitat, *Hereditas*, **3**: 211–350, 1922.

tion. A morphologically distinguishable ecotype is equivalent to a subspecies or geographical race.

A *biotype* is a population consisting of individuals with identical genetic constitution. It is of no recognized taxonomic importance.

A *modification* is a nonhereditary difference caused by the direct action of the environment in influencing growth. A modification may be confused with hereditary differences such as mark the biotype or even the ecotype and can only be distinguished from these by comparing the plants when grown in the same environment. Like biotypes, modifications have no taxonomic standing.

Since herbaria and botanical manuals the world over use generic and specific names based on morphology, it is not expected that these will be replaced soon by other names based on experiment, but it is hoped that revision by the experimental method will gradually correct the many errors in nomenclature that now exist. Certainly this newer work gives a deeper insight into the mechanism of evolution.

MAJOR AND MINOR CHARACTERS

The higher plants are so complex and have so many different characters that the early botanists were greatly perplexed to know which features were important for taxonomic purposes and which unimportant. Naturally those of greatest importance would be used as a basis for main divisions and those of lesser importance for the subdivisions. They made the fundamental mistake of classifying the higher plants primarily into trees, shrubs, and herbs. Each of these was then subdivided into smaller groups. The beginning student in systematic botany has a similar problem. He wishes to know which characters should be family distinctions, which are the ones used for separating genus and species, and which are too trivial or too unreliable to have a taxonomic value.

In modern taxonomy an effort is made to have the larger groups, *e.g.*, classes, show the more ancient phylogenetic branchings and the smaller groups, *e.g.*, genera and species, show the more recent branchings. The question then arises: Which morphological characters indicate ancient and which indicate recent origin? These points have now been fairly well established, and

the student of today can be guided to some extent by studying the classifications and the analytical keys in use and noting the characters used for distinctions between classes, families, genera, species, etc.

In classifying the Spermatophyta we now recognize the covering of the ovules, number of cotyledons, and arrangement of the fibrovascular bundles as major characters used for making classes and subclasses, while size and shape and surface coverings—hairs, etc.—are minor characters used in making species. Inflorescences, arrangement of leaves on the stem, and union of floral parts have an intermediate rating.

Stability.—Almost without exception the more stable structures or characters, such as those listed above as major, are results of ancient evolutionary departures. This means that groups that differ with respect to these structures have existed for a relatively long time. On the other hand, the unstable qualities, such as length of stem, fleshiness of root, hairiness, and color of petals, indicate more recent changes and may be quite variable.

Vegetative versus Reproductive Structures.—The older classifications were based mostly on vegetative parts, no *especial* attention being given to flowers and fruits. Linnaeus, about the middle of the eighteenth century, strongly emphasized the advantages of using reproductive parts in classification. He used no vegetative characters for describing genera. The great French botanist, A. P. de Candolle, who lived a generation later, followed the same plan. At the present time morphological characters of all kinds are used, but the reproductive parts are most emphasized. Practically the only vegetative structures of major importance for purposes of taxonomy are those of the fibrovascular system of stems and leaves. Carpels, stamens, petals, and receptacle are of almost equal rank with fibrovascular structures and because of their greater variety have a much wider range of usefulness.

Clear-cut versus Intergrading Characters.—Those major characters that are used for dividing the spermatophytes into classes have long ago reached a state of equilibrium. They are now clear-cut. Intergrading conditions between flowering and flowerless plants and between the enclosed and the naked ovules can be imagined and may have existed at one time but apparently do not exist now. Likewise, the characters used for dividing the

class angiosperms into the subclasses monocotyledons and dicotyledons—*viz.*, number of cotyledons in the seed, distribution of vascular bundles in stems, and character of venation in the leaves—show very few intergrading forms at this time. Minor characters, however, are very likely to be intergrading. There may be every degree of pubescence, of floral coloration, and of size and shape of leaves. Some gradations are clearly expressions of environment. It is likely that others express evolutionary branchings so recent that the types have not yet become fixed. They may be merely differences of degree and represent a

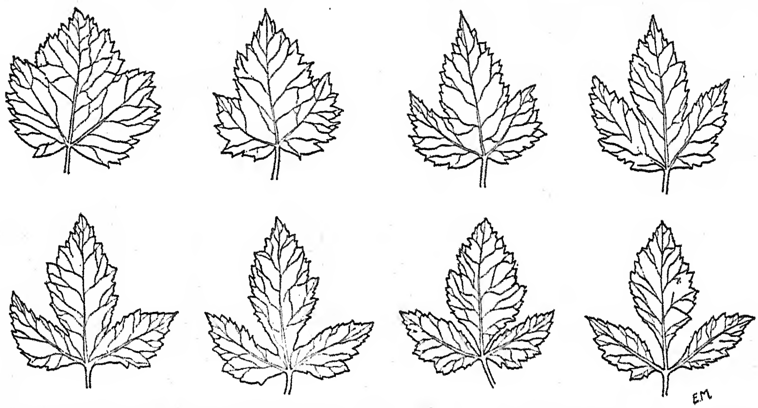


FIG. 94.—Intergrading characters. Leaves from a single shrub of mountain maple showing different degrees in the extent to which the margins are cleft. Every gradation between any two of the leaves shown above can be found.

condition in which certain individuals, strains, varieties, or species have advanced farther than others in the same category.

It is common taxonomic practice, based on experience and reason, to hold more closely to major than to minor characters. If a plant shows any departure whatever from a written description with regard to a major character, it is usually rejected at once from that group. If it fails to agree in an intermediate character, such as number of petals or dehiscence of fruit, the identity is strongly questioned. The plant may, however, differ, in degree at least, in one or two minor characters; but the more of these it violates, the more doubt is thrown upon the identity. It may be said in this connection that related species sometimes hybridize in nature, thus increasing the difficulty of identification. Certain oaks and willows are examples.

Homologues versus Analogues.—Morphological comparisons may mislead one unless he has a fundamental understanding of homologous and analogous parts. Structures similar in appearance and function may be homologous, *i.e.*, specialized from the same part of the plant—root, stem, or leaf—or they may be only analogous, *i.e.*, specialized from different parts. All leaf structures may be regarded as homologous with each other, and likewise all stems and all roots, regardless of their degree of

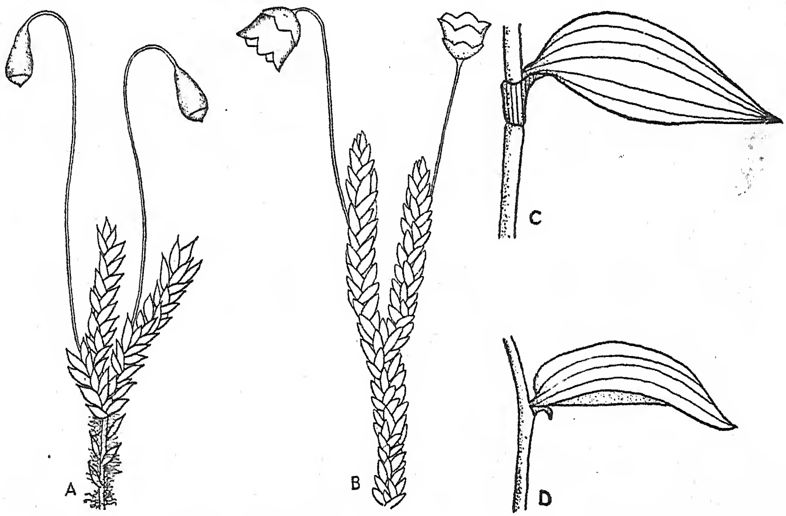


FIG. 95.—Analogous structures. *A*, moss plant. *B*, white heather. The leaf-like structures of the moss plant are parts of the gametophyte, while those of white heather are parts of the sporophyte. *C*, leaf of wandering Jew. *D*, cladophyll of greenhouse smilax. The cladophyll, although leaf-like in appearance and function, is a specialized stem, borne in the axil of a scale-like leaf. Although similar in appearance, analogous structures do not indicate relationships.

specialization. In the case of leaves, homology may apply to parts rather than to entire leaves. Thus the thorns of the black locust are homologous with stipules, while thorns and tendrils of other plants may be homologous with petioles or with stems. However, a leaf structure can be only analogous to stem or root structures, and stem structures may be analogous but not homologous to leaves or roots. The leaf-like cladophyll of common greenhouse smilax is analogous to the true leaf, as is also the so-called leaf of the moss, which is a part of the gametophyte generation. Analogous structures are similar in appearance, but

homologous structures may or may not resemble each other. The cladophyll just mentioned, the thorn of the hawthorn, and the tuber of the potato are all homologous with stems. It may be stated as a general proposition that where the structures performing a given function in two plants are only analogous, these plants are not closely related. For example, it is rare to find in the same genus one plant with tendrils that are specialized stems and another with tendrils that are specialized leaves. The same may be said with regard to thorns. Likewise, large, colored, petal-like bracts do not usually occur in the same genus with large-petaled flowers. Analogous structures are rather strong, then, in

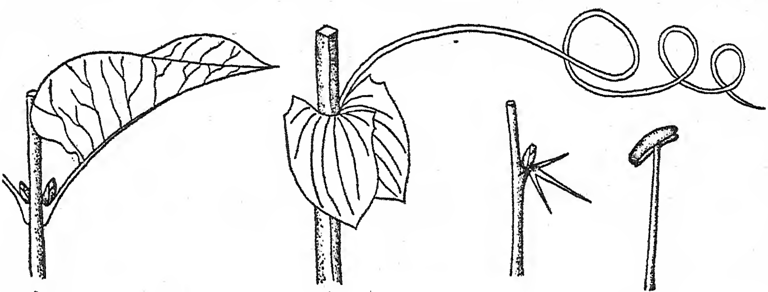


FIG. 96.—Homologous structures. *A*, leaf of lilac. *B*, tendril of yellow vetchling between two large stipules. *C*, thorn of barberry. *D*, stamen of lily. All are homologous structures, *i.e.*, they have a similar origin and are all potentially leaves. A comparison of homologous structures is significant in determining relationships.

indicating differences. No very general rule can be laid down, however, for homologous structures. They are so numerous and so varied that they may indicate any degree of relationship.

Special Structures.—Remarkable development in one direction characterizes certain plants, notably the devices for catching insects, the floral structures of the orchids, and various xerophytic adaptations. These must be regarded as moderately strong characters for purposes of classifying the plants possessing them, but they have a very limited application.

Habitat.—Many descriptions of specimens include the habitat. This has value as a suggestion but is treacherous as a character for classification, since the agencies for plant distribution may carry some individuals far from their usual haunts. Under these circumstances there may be considerable variation from the written description of the species, for environment determines in

some measure the size, breadth of leaves, succulence, hairiness, etc.

Ease of Comparison.—For generations botanists have fought a tendency to give undue importance to certain superficial characters that results in artificial groups. It may have been found convenient to call all the lower plants that have no chlorophyll, fungi; all plants below the liverworts, thallophytes, and all woody plants with staminate flowers in catkins, Amentiferae; but to regard any of these groups as phylogenetic units, in the light of present knowledge, is a monstrosity on a par with classing butterflies and bats with birds. Tendencies of this kind on a smaller scale are numerous. Such artificial groups may be recognized under common names, such as fungi and seed plants, but we should, where possible, avoid such technical or scientific names as Hyphomycetes and Thallophyta. Hyphomycetes and Amentiferae are now practically obsolete terms, and Pteridophyta and Thallophyta may become so. One of the greatest duties of the systematic botanist is to perfect the natural system of classification and to present it in a form that will be scientifically correct and yet convenient enough to gain recognition in a world where efficiency is a valued attribute.

CHARACTERS OF SPERMATOPHYTA

It would be very convenient if we could say that one character is always used for class distinctions, another for family distinctions, another for generic distinctions, etc. Were plants perfectly standardized in their morphology, this could be done; but they are not. We must, therefore, make the best of conditions as we find them. It is so desirable, however, to give the student some idea of the methods by which the different categories are distinguished that a discussion of the values and uses of the more prominent characters will be given.

Probably all botanists agree that a phylogenetic arrangement of the flowering plants is like the trunk and branches of a tree. One conception of it is illustrated in Fig. 92, page 238. It is important to remember in this connection that the same character (*e.g.*, apetalous or unisexual flowers or united carpels) sometimes appeared later in one group or phylogenetic branch than in another, as a separate evolutionary act, and may therefore be used either as an ordinal, a family, or a generic distinction. Most

important of all in interpreting the significance of different characters is the fact that phylogenetic groups are based not on *single* characters but on *combinations* of characters. To divide the angiosperms into two subclasses, one consisting of all plants having simple leaves and the other of all plants having compound leaves, with no other characters in common, would be absurd and unquestionably artificial.

Roots.—When bulbs, tubers, rhizomes, etc., which are not properly parts of the root system, are excluded, underground parts have but a limited taxonomic value. Roots are hard to observe, and, having no division into nodes and internodes, they are relatively characterless. Also, they are much affected by the character of the soil. For these reasons many descriptions make no mention of roots, and they are practically never used for specific or generic distinctions, though in some families, such as Cruciferae, taproots are the rule, while in others, such as Gramineae, the roots are mostly fascicled.

Probably the most usable character of roots is their longevity. On this basis plants are divided into annuals, biennials, and perennials. The strength of this character varies considerably, being mostly a family, a generic, or a specific distinction.

Stems.—In early times stems were very much used in classifying plants, and even today their importance is not minimized. One of the most dependable characters found in higher plants is the distribution of fibrovascular bundles. It is generally agreed that, if spermatophytes only are considered, the arrangement in a cylinder, illustrated by the gymnosperms and the dicotyledons, is the more primitive form, and the scattered arrangement in the monocotyledons is derived from it as a more recent departure, although we must concede the likelihood that remote fern-like ancestors of the gymnosperms had scattered bundles also. The number of leaves and buds at the nodes may be looked upon as a character of the stem rather than of the leaf. This character is of intermediate value, being usually a family or generic distinction, but it is sometimes specific. Actually there are some plants the lower leaves of which are alternate and the upper leaves opposite. The degree of lignification and the longevity of the stem, distinguishing trees and shrubs from herbs, are now regarded as intermediate characters. Some families are wholly woody and a very few wholly herbaceous, but most of them are mixed, having

both woody and herbaceous members. The distinction is usually a generic one. Ancestrally, the woody stem is the older. Branching habit is a very weak character, often determined by environment and seldom used for categories larger than species. The trailing habit of vines is an intermediate character of generic or family importance.

Leaves.—The taxonomic value of leaves is about on a par with that of stems. Primitive leaves were probably simple rather than compound and had branched or netted veins. The venation is a character of major importance, being one of the distinguishing features between dicotyledons and monocotyledons. It should be mentioned, however, that a few of the monocotyledons, as *Smilax* and *Trillium*, have netted-veined leaves, though the venation here is closed rather than open. The compounding of the leaf is an intermediate character. Usually it is a family or even an ordinal distinction, but sometimes it has only generic value. In the family Rosaceae, particularly, there is a lack of uniformity. The fact that some leaves are persistent and others deciduous is often of value in classification. The evergreen condition, *i.e.*, having persistent leaves, is generally recognized as primitive, although it is probable that some evergreen angiosperms had deciduous ancestors. The character has usually a generic value as there are no large families of angiosperms entirely evergreen.

The form of simple leaves is a weak character, generally used along with others to distinguish species.

Epidermal hairs are considerably used for specific distinctions, but they have little value for the higher categories.

Inflorescences.—Mention has been made of the strong modern tendency to emphasize reproductive structures in taxonomy. No doubt the solitary flower, probably typifying the strobilus or cone of the pteridophytes and gymnosperms, is more primitive than the collective inflorescence. Inflorescences have an intermediate rating usually of generic value, although some families are uniform as to type. Some trouble is given here by intergrading characters, since racemes grade into spikes and both racemes and spikes grade into heads. A few inflorescences are complicated by the fact that small flower clusters are so arranged that larger inflorescences are thus formed. The heads of certain members of the Compositae may be single, as in the sunflower, or they may be

arranged in panicles, as in yarrow. In the Gramineae the spikelets may be arranged in panicles, as in oats, or in spikes, as in timothy.

Flowers.—In comparative morphology the flower is usually regarded as a specialized strobilus, in which the lower sporophylls have become sterilized to form sepals and petals and the upper have changed into stamens and carpels. Unfortunately, fossil remains that show the details of transition are wanting. The axis of the strobilus is shortened to form the receptacle of the strobiloid or hypogynous flower of the primitive type. This occurs regularly in lower monocotyledons and lower dicotyledons. In the cotyloid or epigynous flower of the higher monocotyledons and dicotyledons, the axis is actually depressed into a cup containing the carpels. This is usually an ordinal or subclass distinction, but in some of the transitional families there is lack of uniformity among genera.

Aside from the flower axis the carpel is the most important organ taxonomically. It is the unit structure of the gynoecium. The primitive condition is that of many separate carpels, reduction in number and union to form a compound pistil being a later development. Basing our evidence on the fossil record and on recent studies of the floral vascular anatomy, we may learn of the probable origin of carpels and of their organization into the various ovary types.

It is generally accepted that the primitive angiosperm carpel, as it existed in prehistoric ages, consisted of a modified leaf-like structure with ovules borne along the margins. These primitive carpels contained a midrib and two marginal veins extending upward from the base. The ovules were attached to the marginal veins (Fig. 97*a*). As ages passed, such a structure is believed to have folded together with the ovules inside. The result was a simple ovary, having a single cavity and a parietal placenta (Fig. 97*b*), *i.e.*, one situated on the ovary wall. This is the simplest type of pistil and is found today in members of the pea family, for example. In the buttercup family and about half of the rose family there are four or more, usually many, simple pistils on a common receptacle, comprising the gynoecium of a single flower.

A compound ovary represents the union of two or more simple ovaries. It has, typically, as many placentae as there are carpels, but it may have either one seed chamber or more than one. In

tracing the evolution of the compound ovary it may be assumed that there was a gynoecium of separate carpels (three in this instance, as indicated in Fig. 97*c*), which united with their placentae toward the center. The result was a three-chambered compound ovary having axial placentation and three seed chambers (Fig. 97*d*). From this type of compound ovary a second type has been derived by the withdrawal of the partitions and the

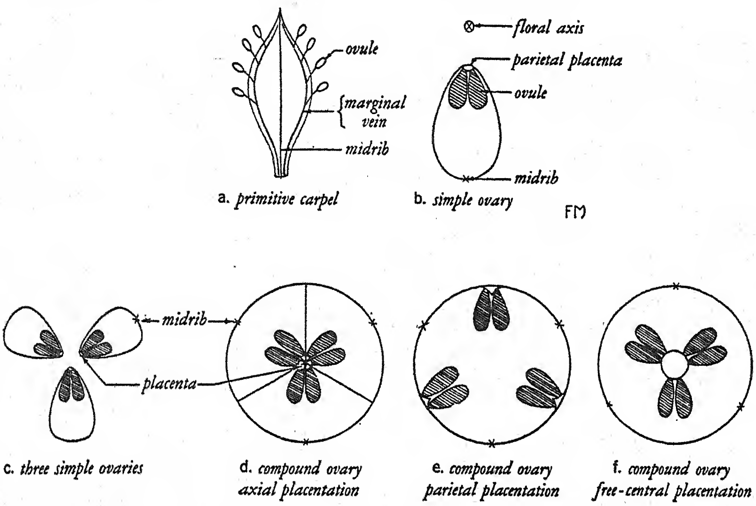


FIG. 97.—One conception of the evolution of the compound ovary from isolated carpels—three in this case. The primitive ovary *a*, a flat leaf-like cladophyll bearing ovules on marginal veins, folds up to form a simple ovary *b*. In this case three such ovaries form *c*, but in others the number varies. By symphysis the simple ovaries become united with axial placentation *d* or with parietal placentation *e*. A further evolution of the axial placentation is the failure of the septa to develop, owing to reduction of the inner carpellary walls, giving free-central placentation *f*. If the central axis to which the ovules are attached in *f* is shortened, basal placentation results. (*Drawings contributed by Miss Florence Mekeel of the Bailey Hortorium, Cornell University, and designed by G. H. M. Lawrence.*)

three placentae until the septa have disappeared and the placentae are situated on the inside of the ovary wall. The result is a three-carpellate compound ovary having one seed chamber and parietal placentation (Fig. 97*e*). A third type is also derived from the type having axial placentation and differs from it in the absence of the cross partitions, the ovules and their placentae remaining at the center on a central column (Fig. 97*f*). The placentation of this latter type is called free-central. An advanced evolutionary development over the free-central type of

placentation exists in the pigweed and buckwheat families, where reduction of the central column has left only a single ovule borne at the base of the ovary. While a plausible explanation is given here for the evolutionary development of the types of compound ovary, it should be remembered that there are other means by which the same end may have been achieved; *e.g.*, it is probable that in some plants the parietal type of placentation may have been evolved from the marginal union of several, open, primitive carpels rather than as here outlined.[1]

Carpellate variations are, for the most part, major characters used for ordinal and family distinctions, though in respect to certain details, such as number and length of styles, a lesser rating must be given them.

Stamens are of considerable importance in classifying plants. Decrease in numbers, union of filaments, and sterility of anthers are among the newer evolutionary developments. They have an intermediate rating, usually for family or generic distinctions. The point of insertion relative to the petals is of considerable importance. Absence of pistils or stamens, resulting in unisexual flowers, may be looked upon either as degeneracy or as a form of specialization whereby the likelihood of close pollination is reduced. It is generally either a family or a generic distinction.

The perianth is usually regarded as part of the system of strobilate leaves that long ago ceased to produce spores. The calyx is rarely absent but presents so little variation that its taxonomic value is limited. Color, other than green, is a derived quality. The corolla is much used in classification. It is relatively easy of observation, and it presents much variety. In primitive flowers it takes the form of many separate petals symmetrically arranged on the receptacle and each similar in appearance to the others in the same flower. Their union to form gamopetalous flowers must be given a variable rating. Whole orders show this character in the higher dicotyledons, but it has developed to a limited extent elsewhere in families otherwise polypetalous. Apetaly is a somewhat weaker character of family, generic, or even specific distinction. Irregularity of corolla is usually a family distinction but may be generic. The color of petals is usually a weak character. The orange and deep-yellow colors are quite dependable, but

[1] This explanation was contributed by G. H. M. Lawrence of the Bailey Hortorium, Cornell University.

gradations from white through pale blue or purple to violet are common and may be misleading.

Pollen Grains.—Taxonomists have been prone to overlook an important set of morphological characters, those of the pollen grains. Considerable research has been carried on in this field, and it has been shown that pollen characters are reasonably con-

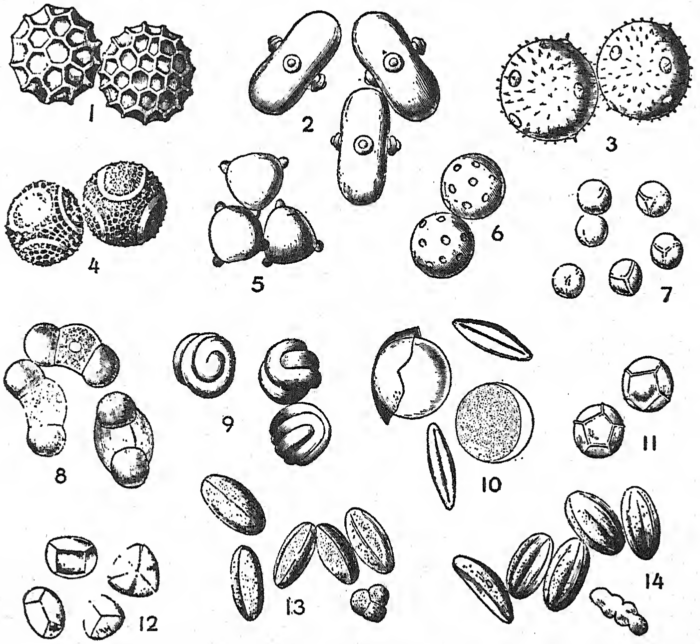


FIG. 98.—Pollen grains of different species of plants. 1, *Cobaea scandens.* 2, *Morina Persica.* 3, *Cucurbita Pepo.* 4, *Passiflora kermesina.* 5, *Circaea alpina.* 6, *Convolvulus sepium.* 7, *Cannabis sativa.* 8, *Pinus Pumilio.* 9, *Mimulus moschatus.* 10, *Albuca minor* (dry and moistened). 11, *Dianthus carthusianorum.* 12, *Corydalis lutea.* 13, *Gentiana rhaetica.* 14, *Salvia glutinosa.* (*After Kerner.*)

stant for each species and that related species generally have grains quite similar in certain respects. Keys to families have been made based on pollen characters alone.[1] The chief characters of pollen grains are size, general shape, germinal apertures, and surface markings, such as spines, ridges, and furrows. It will be noted that, while most morphological characters of higher plants are expressions of multicellular structures, those of pollen

[1] See R. P. Wodehouse, "Pollen Grains," McGraw-Hill Book Company, Inc., 1935.

grains are characters of the individual cell. These have long been used in classifying the lower plants, especially the fungi. In addition to the morphology of individual grains, the pollen masses show considerable variation, in some being powdery and in others waxy or viscid. Pollen characters have family, generic, and specific value.

Fruits and Seeds.—For purposes of analytical keys it is best not to depend too strongly on fruits and seeds, for much identification is done with immature plants. Indeed, it is often annoying to find fruit characters used in analytical keys. Although some of these characters, such as the numbers of seed chambers and ovules, can be determined from the flower pistils or young fruits, other qualities such as size, color, fleshiness, and dehiscence of fruits and size, shape, and markings of seeds develop later. These are for the most part rather weak characters, with the exception of the method of dehiscence. More dependable characters are the number of cotyledons, the presence or absence of endosperm, and the position and shape of the embryo.

A special art has been developed recently in agricultural work—that of identifying plants, particularly weeds, by seed characters alone. Skill in this field has considerable value in detecting impurities in seeds of cultivated plants. In some cases seed characters are sufficient to distinguish species; in others only generic identification is feasible.

Starch Grains.—Flowering plants show almost endless variety in the size, shape, and structure of their starch grains. Even in different species of the same genus clear-cut differences are often found. They are not much used in taxonomy, but by means of them adulterations of starches and starchy products are often detected with the microscope. Their use for the identification of species has future possibilities.

Morphological Indicators of Phylogeny.—To facilitate piecing together our morphological data into a phylogenetic system of classification we need to know many details of the trend of evolution. This knowledge has been derived slowly, but now there is rather uniform agreement on the following principles:[1]

[1] Most of these rules were stated in slightly different form by Charles E. Bessey, The Phylogenetic Taxonomy of Flowering Plants, *Ann. Mo. Bot. Gard.*, **2**: 109–164, 1915. A few others have been added by Alfred Gundersen, Evolution in Flowering Plants, *Brooklyn Bot. Gard. Leaflets*, Ser. XI,

1. Plant relationships are up and down genetic lines, and these must constitute the framework of phylogenetic taxonomy. This will naturally form a branching but not a reticulate structure, except in the formation of species and varieties by hybridization.

2. Some evolutionary processes are progressive (upward) while others are regressive (downward, "degenerative").

3. Evolution does not necessarily involve all organs of the plant at one time or in the same direction. One organ may be advancing while another is stationary or retrograding.

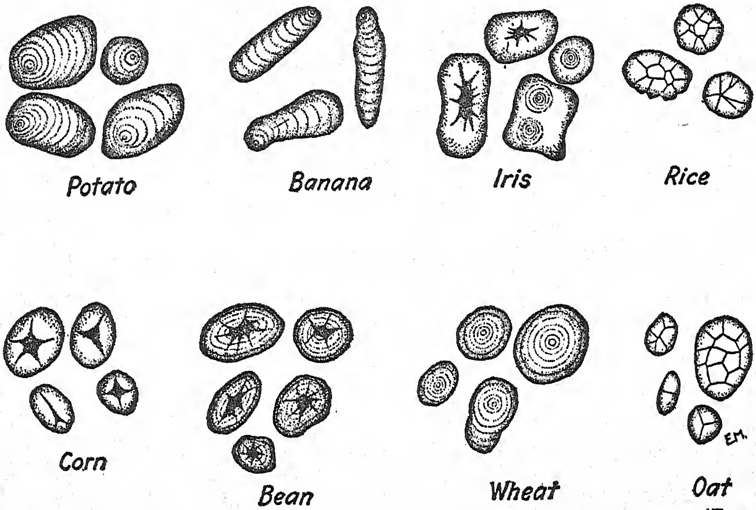


FIG. 99.—Eight kinds of starch grains showing differences in appearance. (*From "Plant Life," D. Van Nostrand Company*, 1942.)

4. Evolution has generally been consistent, and when a particular progression or regression has set in, it has persisted for generation after generation.

5. In any natural group the chlorophyll-bearing plants precede the non-chlorophyll-bearing ones.[1] Saprophytes were derived from independent forms, and parasites usually from saprophytes among the lower plants and from independent forms among the flowering plants.

No. 9, 1923; and by J. Hutchinson, "The Families of Flowering Plants," pp. 6 and 7, Macmillan & Company, Ltd., 1926.

[1] Exception should be made of the most ancient primitive life, which probably possessed no chlorophyll, since its production had not yet evolved. Many believe that the bacteria and the blue-green algae had a common ancestry lacking chlorophyll.

6. Among the seed plants the stem structure with collateral bundles arranged in a cylinder is more primitive than that with scattered bundles.

7. Tracheids are more primitive than vessels (tracheae).

8. Scalariform vessels are more primitive than vessels with round pits.

9. In most groups of seed plants woody members have preceded the herbaceous ones.

10. In most groups of seed plants erect members have preceded the vines.

11. Perennials are more primitive than biennials, and biennials are usually more primitive than annuals.

12. Historically, leaves were first persistent (evergreen) and later deciduous. However, evergreen angiosperms were probably derived from deciduous angiosperms.

13. The spiral arrangement of leaves on the stem preceded that of the opposite and whorled types.[1]

14. Spirally imbricate floral parts are more primitive than those that are whorled and valvate.

15. In angiosperms simple leaves are more primitive than compound leaves.

16. Among the seed plants the netted venation of leaves is more primitive than the parallel venation.

17. Usually structures with many similar parts are more primitive, and those with fewer and dissimilar parts are more advanced, *i.e.*:

a. The many-parted flower is the more primitive, the type with few parts being derived from it, and the change is accompanied by a progressive sterilization of sporophylls.

[1] This is the statement given by Hutchinson. Bessey had earlier stated, "Historically the arrangement of the leaves in pairs on the stem is held to have preceded the spiral arrangement in which the leaves are solitary at the nodes." This is reasoned from the fact that in dicotyledonous plants the first leaves (cotyledons) of the embryo are formed two at a node while in the monocotyledonous plants there is but one at a node.

As a matter of fact, many families in both monocotyledons and dicotyledons contain some species with one arrangement of the foliage leaves and other species with the other arrangement, sometimes both in the same genus. Also, some individual plants have one arrangement of the lower leaves and the other arrangement above. It is evident, therefore, that the change from either arrangement to the other is an easy one. For this reason the principle must be applied with discretion, although it has value in a study of floral organs.

b. A condition in which the perianth consists of like segments is more primitive than one in which sepals and petals are unlike each other.

c. Regular flowers preceded irregular ones.

d. Flowers with petals preceded apetalous ones, the latter being derived by reduction.

e. Numerous carpels represent a more primitive condition than few carpels.

f. The presence of numerous stamens indicates a more primitive condition than that of few stamens.

g. Evolution in angiosperms is believed to have proceeded from seeds with two coats to those with only one.

18. Symphysis of parts is an advanced character, *i.e.*:

a. Polypetalous flowers are more primitive than gamopetalous ones, the latter being derived from the former by symphysis.

b. Separate stamens preceded united stamens.

c. Separate carpels represent a more primitive condition than united carpels.

19. Hypogyny is the primitive condition and from it perigyny and epigyny have been derived.

20. In most cases at least, the solitary flower is more primitive than the inflorescence.

21. Bisexual flowers preceded unisexual flowers, which were derived from them by reduction.

22. The monoecious condition is earlier than the dioecious.

23. Simple and aggregate fruits preceded multiple fruits.

24. The primitive seed contains endosperm and a small embryo; the advanced type has little or no endosperm, and the food is stored in a large embryo instead.

25. A straight embryo is usually more primitive than a curved one.

26. The same evolutionary phenomena have often been repeated as separate occurrences at different times and in different parts of the plant kingdom. This statement refers to loss of chlorophyll, loss of petals, stamens, and carpels, acquisition of fleshy texture in fruits and of various types of thorns, change from simple to compound leaves, from erect to prostrate habit, and from hypogynous to perigynous or epigynous insertion of floral parts, and lateral union (symphysis) of petals, stamens, and carpels.

27. In determining the closeness of relationship between two

families or other groups it is usually best to compare with each other the more primitive, or basal, members of each group, rather than those that are most highly specialized or those that are simplified by reduction.

Some of these rules are statements of established facts, while others must be looked upon as general principles with probable exceptions. Most phylogenetic systems of taxonomy conform to these principles, and they should serve as guides to every student in the analysis of such systems.

In summarizing this discussion several points are to be emphasized: (1) that in defining the different groups of plants, combinations of characters must be considered; (2) that evolution has caused certain characters such as unisexuality, irregularity of flowers, compounding of leaves, and saprophytism to appear repeatedly and independently in different groups; (3) that occasionally, perhaps by coincidence, similar combinations of characters appear in different groups, resulting in like individuals of different ancestry (polyphyleticism); (4) that there have been certain general tendencies in the evolution of the flower, notably reduction in number, fusion, and specialization of parts; and (5) that only approximate taxonomic values can be attached to most of the characters used for classification.

Single Characters versus Combinations of Characters.—In the beginnings of our present system of classification the tendency was to base a group of plants on a single character and to use this character to distinguish it from all other groups. Thus we had, as the primary groups of flowering plants, trees, shrubs, and herbs, regardless of floral and leaf characters. Even as late as the eighteenth century Linnaeus prepared a system of classification based chiefly on single characters such as number of stamens (see page 285).

Gradually botanists came to realize that all, or at least many, characters must be taken into consideration jointly in determining what plants make up a class, family, genus, or other category. To get a full comprehension of this fact the student should turn to the descriptions of families given in Chap. VII and VIII. There he will discover, if he has not already done so, that there is scarcely any morphological character that all members without exception have in common, but the combinations of characters found bind the species into one family.

CHAPTER XI

SYSTEMS OF TAXONOMY

It is difficult to appreciate the strength and weakness of our modern systems of classification without a knowledge of the struggle by which they came into being. Students at first assume that botanists have reached perfection in classification and nomenclature; then, as a sequel to disillusionment brought about by the discovery that there is some disagreement, they are prone to emphasize the failings and minimize the virtues unless they are made to realize the immensity of the problem and the handicaps under which the makers of systematic botany labored.

Nomenclature Preceded Taxonomy.—There can be no doubt that people gave names to certain plants before they attempted to classify them. The first were, of course, common names in many languages and tongues. With the limited intercourse that then prevailed among peoples and the entire lack of scientific work requiring exact terminology, these common names and the loose application of them were sufficient. No need was felt for a formal classification.

PRE-EVOLUTIONARY SYSTEMS OF TAXONOMY

Through all the centuries prior to Darwin's "Origin of Species" (1859), botanists used no one outstanding basis for classification. Up to the sixteenth century they drifted like a ship without a rudder, with classifications based on economic uses of plants predominating. Then, gradually, morphology came into recognition as superior to other taxonomic criteria, not at first because it was known to indicate phylogenetic relationships, for these were not known to exist, but because it coincided most closely with a feeling or instinct for "natural affinities."

Taxonomy Began with the Greeks.—There are some who believe that the ancient civilizations of China and Egypt had made considerable advancement in systematic botany and the medicinal uses of plants, but if so their work had no influence

on these subjects as we know them. The foundations of systematic botany as we know it today were laid by the Greeks, notably Theophrastus and Dioscorides. Beginning several centuries before the Christian Era, the Greek physicians found in some plants actual medicinal properties not to be confused with superstitious beliefs. The fame of this work spread to the Roman Empire and other parts of Europe and created a desire for what we would now call an international system of nomenclature and taxonomy. The grouping was at first largely an economic one, however, and the nomenclature became a heterogeneous mixture of Greek, Latin, and other names, varying with the country using it A few of the names still survive.

Aristotle, and more particularly his pupil Theophrastus, made some attempt to extend botanical knowledge beyond the scope of medicinal plants. Theophrastus[1] has well been called the Father of Botany. Although his writings were made some 300 years before the birth of Christ, they were incomparably better than any others before the sixteenth century of the Christian Era. He clearly recognized several hundred species and a few families, although he had no system of categories such as are used today for classification. These Greek pioneers made the fundamental mistake of trying to make life processes the basis of classification; and the structures for carrying on these processes about which little was known were given a rating according to the importance of the physiological process. Nutrition was considered the most important; hence vegetative structures—unspecialized roots, leaves, and stems—were used for the main subdivisions. The writings of the Greeks embodied too few observations on what plants are and too much philosophizing as to how they might be expected to be.

Taxonomic Development in Southern Europe.—The work begun by the Greeks languished for a time and was then revived, culminating in the philosophy and classification of the Italian, Cesalpini, in the sixteenth century. He wrote a set of sixteen volumes on plants. The first was philosophical, making much of such minor distinctions as cultivated versus wild plants, trees versus shrubs versus herbs, and using curious mixtures of

[1] Theophrastus' "Enquiry into Plants," an English translation, shows an astonishing amount of botanical knowledge, along with some faulty deductions.

morphology and medicinal virtues. In the fifteen other volumes he divided the plant kingdom into fifteen heterogeneous groups including some animal forms. Cesalpini's work was remarkable in its attempt at that early date to classify the whole plant kingdom, and it made a profound impression on the botanists of southern Europe, but it lacked a consistent morphological basis and little of it has survived.

Taxonomic Development in Central Europe.—Systematic botany in the central European states followed a course that was somewhat different from that developed in southern Europe. The botanists of this central region, particularly those of Germany and Holland, were striving, first, to find and identify the medicinal plants of the Greeks and to add to the number, and then to gain greater knowledge of plants in general. To this end they studied the writings of the ancients, made extensive collections, wrote exhaustive descriptions (sometimes with illustrations), established botanical gardens, and, finally, as a result of laborious comparisons, they began to make classifications. In their first attempts they did little abstract reasoning but followed rather closely morphological similarities and differences and, like Theophrastus, showed quite accurate perceptions of "natural" groupings, even though they were not at that time guided by a knowledge of evolution. The strength of their work lay in their numerous and closely comparative observations and in the predominance of morphological characters over economic distinctions. Slow and ponderous thinkers, they did not quickly formulate complete classifications; but certain groups such as Umbelliferae, Leguminosae, Gramineae, Labiatae, Malvaceae, and a part of the Compositae became quite definite entities—oases, as it were, in the desert of unclassified plants, or crystals forming in an indefinite solution.

Some incidental contributions to taxonomy are worthy of note, especially the illustrated herbal of Brunfels (1530), the descriptive materia medica of Bock (Tragus, 1530), and the glossary of technical terms by Fuchs (1542), each work the first of its kind worthy of mention in botanical literature. It is evident that the Holland botanist, de Lobel, sensed quite keenly the natural relationships of plants; for in his work, written toward the end of the sixteenth century, he grouped many plants correctly, though submitting no formal system of classification.

His writings probably had much influence on the systems of de Jussieu and his contemporaries.

Gaspard Bauhin, a Swiss botanist, climaxed forty years of arduous work in systematic botany with the publication of "Pinax" in 1623, in which he described some 6,000 species. This publication had the great merit of using generally the binomial system of nomenclature and has proved to be a valuable book in tracing synonyms. While Bauhin did not set forth the special value of the binomial system or urge uniformity in its adoption, there is little doubt that his work stimulated Linnaeus to do so later.

Fortunately, there appeared in this science, as in others, a few early European workers who had a clear insight into some of the principles involved, and who, step by step, worked out a plan of classification that we now accept for the most part as sound and reliable. By rejecting the errors and retaining the good points brought out by their predecessors and contemporaries they established many of the important groups of the plant kingdom as we know them today. A few more significant men and their works will be mentioned, but most of them will have to be omitted.

John Ray.—The botanists of western Europe (England and France), following the morphological method to the exclusion of philosophy and economic usage, were active in organizing the fragmentary findings into definite systems. The English botanist, John Ray, in his "Historia Plantarum," completed in 1704, proposed a system, certain portions of which have survived to the present day:

I. Herbae
- *a.* Imperfectae (flowerless)
- *b.* Perfectae (flowering)
  - Dicotyledones (with two cotyledons)
  - Monocotyledones (with one or no cotyledon)

II. Arbores
- *a.* Monocotyledones
- *b.* Dicotyledones

These main groups were subdivided into thirty-three smaller ones, some of which corresponded fairly closely to our present families. Others were heterogeneous, including even animals.

The conspicuous error of Ray's system is faulty subordination in giving major value to the distinction between woody and herbaceous stems, as did the Greeks and Romans before him. Its lasting value lay in its distinction between monocotyledons

and dicotyledons, and to that extent it became one of the great foundation stones of our present classification.

Carolus Linnaeus.—The greatest contributor to systematic botany up to the middle of the eighteenth century was Linnaeus. A native of Sweden, he traveled throughout Europe visiting other botanists and making extensive comparisons of flora; and being a brilliant thinker, he was able to combine, with great powers of discrimination, the work of his predecessors and contemporaries, most thoroughly sorting the wheat from the chaff. His chief contributions were to nomenclature, those to taxonomy being indirect, for he never proposed a system of classification at all satisfactory to himself or of lasting value. He did, to be sure, publish an artificial system based almost exclusively on floral characters, the stamens being given a preponderance of attention; but the insertion of parts—hypogynous, perigynous, and epigynous—received recognition also, and this had a lasting value. Linnaeus realized the imperfections of this scheme and regarded it as a temporary makeshift until a more natural system could be devised. This he began but did not live to complete. His artificial system had the effect, however, of focusing attention on the taxonomic value of floral structures and made a profound impression on the botanists of his time. His "Species Plantarum" (1753), describing all species known at that time, and his "Genera Plantarum" (5th ed., 1754), similarly describing the genera, stand today as the greatest of botanical classics. These works, with his successful promulgation of the binomial system used, but not established, by Bauhin, and his clear-cut conception of species have made his name immortal.

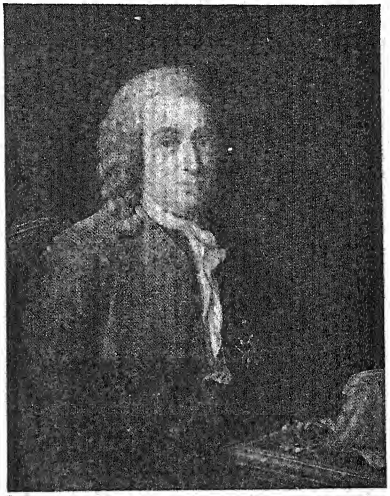


FIG. 100.—Carolus Linnaeus (1707–1778). Great Swedish naturalist. He described and named many plants and animals, laid emphasis on floral structures, and did much to establish the binomial system.

A. L. de Jussieu.—It is generally conceded that the French botanist, de Jussieu, was the founder of the present system of taxonomy, though he took freely from the work of his predecessors. While familiar with Cesalpini's work, he made but limited use of it. He divided the plant kingdom into fifteen classes, fourteen of them seed plants. These in turn were divided into orders, some of which were roughly comparable to our families. His main subdivisions, as published in 1789, are as follows:

I. ACOTYLEDONES. Plants without cotyledons: Fungi, Ferns, Mosses, Algae, Naiades (CLASS I)
II. MONOCOTYLEDONES. Plants with one cotyledon
- 1. Stamens hypogynous (CLASS II)
- 2. Stamens perigynous (CLASS III)
- 3. Stamens epigynous (CLASS IV)

III. DICOTYLEDONES. Plants with two cotyledons
- 1. Apetalae
  - Stamens epigynous (CLASS V)
  - Stamens perigynous (CLASS VI)
  - Stamens hypogynous (CLASS VII)
- 2. Monopetalae
  - Corolla hypogynous (CLASS VIII)
  - Corolla perigynous (CLASS IX)
  - Corolla epigynous
    - Anthers connate (CLASS X)
    - Anthers free (CLASS XI)
- 3. Polypetalae
  - Stamens epigynous (CLASS XII)
  - Stamens hypogynous (CLASS XIII)
  - Stamens perigynous (CLASS XIV)
- 4. Diclines irregulares, male and female flowers on different plants, corolla generally absent (CLASS XV)

It will be seen that de Jussieu abandoned the primary division into woody versus herbaceous stems, gave major consideration to the cotyledons, and made prominent use of petals and stamens. His system lacks modern conceptions in characters of vascular bundles, floral axes, petals, and carpels, but it has served as a basis on which by addition and correction the best systems have been built.

A. P. de Candolle.—De Jussieu's system of classification was extended and improved by A. P. de Candolle (1819), a Frenchman who carried on most of his work in Switzerland. He was unquestionably the greatest botanist of his time and not only improved plant classification but set forth some important principles of taxonomy. To de Jussieu's recognition of the number of cotyledons, character or absence of corolla, and position of stamens

de Candolle added, as a major character, the arrangement of fibrovascular bundles. He also made some progress in the classification of the lower plants.

Stephen Endlicher.—This distinguished systematist, working in Austria, published a pretentious work on plant classification, which was completed in 1840. He followed de Candolle's system to a large extent but subdivided the plant kingdom into more classes and orders (equivalent to our families). He made an effort to group plants above the thallophytes on the bases of apical growth, growth in diameter, or both. This distinction led him to combine gymnosperms with dicotyledons, an error that was later copied by Bentham and Hooker.

FIG. 101.—Augustin P. de Candolle (1778–1841). Great early botanist of France and Switzerland. He contributed much to the rules of nomenclature and gave the world a system of plant classification that was an extension of the one proposed by Jussieu. (*Courtesy of Alfred Gundersen, Brooklyn Botanic Garden.*)

Morphological Discoveries. About this time several important morphological discoveries were made that became serviceable in the classification of plants. Notable among these were Robert Brown's studies on seeds, including the nature of the endosperm and the lack of carpellate coverings for the ovules in the gymnosperms; Endlicher's anatomical studies, showing the manner of growth in stems and distinctions between stem and root; Lindley's investigations of the vascular bundles in stems and leaves; and Hofmeister's embryological studies, revealing among other things the alternation of generations. Hofmeister evidently realized that the alternation of generations established a natural connection between the Bryophyta, Pteridophyta, and Spermatophyta even though Darwin's "Origin of Species" had not yet been published.

Fortified by these morphological discoveries and by a knowl-

edge of evolution, the later taxonomists were able to make very marked improvements.

EVOLUTIONARY SYSTEMS OF TAXONOMY

In the midst of steady progress on the improvement of systems of classification that were purely and blindly morphological, the conceptions of species and other categories and the ideals of classification were profoundly modified by the introduction of the doctrine of evolution.

Charles Darwin.—Probably the most epoch-making event in the entire history of biological science was the discovery of the principle of evolution. That Darwin was not the first to get an inkling of this principle is well known, but with Wallace he seems to have been the first to comprehend its sweeping significance ("Origin of Species," 1859). After the first wave of excitement was over, systematists quite generally accepted the doctrine and began to revise their systems to fit the new principle of phylogenetic relationships. Fortunately, much that had already been done was usable, for all but the morphological systems had been pretty much eliminated from botanical taxonomy, and morphology has proved the best single criterion of phylogeny.

Bentham and Hooker.—These two great English systematists, contemporaries of Darwin, worked out in far greater detail than any of their predecessors a system of classification of the Spermatophyta that for some thirty years dominated the botanical world and has been modified rather than revolutionized to make the systems in use today. It is virtually an extension of the work of de Jussieu and de Candolle.

In their "Genera Plantarum" (1862-1883) they made a rather complete series of categories giving dicotyledons, gymnosperms, and monocotyledons equal rank, equivalent to classes, with the gymnosperms between the other two, for they had not sensed the value of Robert Brown's discovery that gymnosperms have naked ovules. The dicotyledons were divided into three subclasses, the further sequence of categories being series, cohort, order, genus, and species. The cohort was practically equivalent to our order and the order to our family. There were altogether 200 orders (families) beginning with Ranunculaceae and ending with Gramineae, Compositae being near the middle

(No. 88). Probably most systematic botanists of today will agree that this system of Bentham and Hooker should have been perpetuated and amplified rather than replaced by the system of Engler.

Julius von Sachs.—Until nearly the close of the nineteenth century little progress had been made with the classification of the Thallophyta. Following the improvement of the microscope to a point of practical usability, Sachs in 1882 proposed a classification of these lower plants nearly on a par with that of Bentham and Hooker for the spermatophytes, though not so detailed.

THALLOPHYTES

Containing chlorophyll		**Not containing chlorophyll**
	Class I. **Protophyta**	
Cyanophyceae		Schizomycetes
Palmellaceae (in part)		Saccharomycetes
	Class II. **Zygosporeae**	
	Conjugating cells motile	
Pandorineae		Myxomycetes
(Hydrodictyeae)		
	Conjugating cells stationary	
Conjugatae (including Diatomaceae)		Zygomycetes
	Class III. **Oosporeae**	
Sphaeroplea		
Vaucheria	(*Coeloblastae*)	Saprolegnieae Peronosporeae
Volvocineae		
Oedogonieae		
Fucoideae		
	Class IV. **Carposporeae**	
Coleochaeteae		Ascomycetes (including lichens)
Florideae		Aecidiomycetes (Uredineae)
Characeae		Basidiomycetes

The shrewdness of this great Austrian botanist is shown by this phylogenetic classification in which he attempted to bring out the relationships of the different groups of algae to corresponding groups of fungi. While the classification contains some serious mistakes due to the inherent difficulty of the subject and the limited amount of detailed work that had been done on the Thallophyta at that time, the main concept is accepted by many botanists.

A. W. Eichler.—Basing his work on a considerable study of morphology, made in the light of the doctrine of evolution, Eichler (1883) made a classification of the entire plant kingdom.

A. CRYPTOGAMAE
- I. **Division:** Thallophyta
  - I. CLASS: Algae (5 groups)
  - II. CLASS: Fungi (3 groups, including lichens)
- II. **Division:** Bryophyta
  - I. GROUP: Hepaticae
  - II. GROUP: Musci
- III. **Division:** Pteridophyta
  - I. CLASS: Equisetineae
  - II. CLASS: Lycopodineae
  - III. CLASS: Filicineae

B. PHANEROGAMAE
- I. **Division:** Gymnospermae
- II. **Division:** Angiospermae
  - I. CLASS: Monocotyleae (7 orders)
  - II. CLASS: Dicotyleae
    - I. SUBCLASS: Choripetalae (21 orders beginning with Amentaceae)
    - II. SUBCLASS. Sympetalae (9 orders)

Eichler's work covered the entire plant kingdom and arranged the lower plants somewhat more definitely than did that of de Jussieu. His classification was contemporary with that of Bentham and Hooker but much less detailed in the treatment of the flowering plants. It corrected the error of placing the gymnosperms between the monocotyledons and the dicotyledons, but unfortunately it placed together under the "Amentaceae" the catkin-producing trees, including poplars, walnuts, birches, and oaks, which were considered primitive because of their apetalous flowers. Other characters, such as the pistillate flowers, the fruits, and the structure of the wood, throw much doubt

FIG. 102.—Adolph Engler (1844–1930). The most influential taxonomist of his time and author of the great system of classification most extensively used today (*Courtesy of Alfred Gundersen, Brooklyn Botanic Garden.*)

on the closeness of relationship between the members of this group.

Engler and Prantl.—Nearly half a century ago the first volumes of an extensive work by two German botanists, Engler and Prantl, were published (1887–1909). This treatise, "Die natürlichen Pflanzenfamilien," covers the entire plant kingdom. While the authors named did much of the work on the flowering plants many sections throughout the plant kingdom were assigned to other specialists. The Engler and Prantl system is a development of that of Eichler and follows it in many respects. Its usefulness is increased by the publication of Engler and Gilg's "Syllabus der Pflanzenfamilien" (10th ed., 1924), and both are expressions of what is commonly known as the Englerian system. In this system the seed-bearing plants (Spermatophyta) are designated as Embryophyta siphonogama and are further subdivided as follows:

EMBRYOPHYTA SIPHONOGAMA
I. **Subdivision:** Gymnospermae
 1. CLASS: Cycadofilicales
 2. CLASS: Cycadales
 3. CLASS: Bennettitales
 4. CLASS: Ginkgoales
 5. CLASS: Coniferae
 6. CLASS: Cordaitales
 7. CLASS: Gnetales
II. **Subdivision:** Angiospermae
 1. CLASS: Monocotyledonae (11 orders)
 2. CLASS: Dicotyledonae
  SUBCLASS: Archichlamideae (Choripetalae and Apetalae) (30 orders)
  SUBCLASS: Metachlamydeae (Sympetalae) (11 orders)

The numerous orders are further subdivided into suborders, families, and genera.

In this system the woody plants with unisexual, apetalous flowers borne in aments (willows, walnuts, birches, oaks, etc., often called Amentiferae) are treated as among the most primitive dicotyledons. It will be noted that the arrangement of this part of the plant kingdom follows that of Eichler and is considered erroneous by many botanists of today. The work has been recently revised, but the new edition still groups some of the distantly related amentiferous trees together and

assigns them a primitive position. It should be understood that the Engler and Prantl system did not base its phylogenetic conceptions on the "morphological indicators of phylogeny" given on pages 276 to 280 of this textbook, most of which are American conceptions. To base a taxonomic system on these conceptions is to change or reject some important parts of the Englerian system.

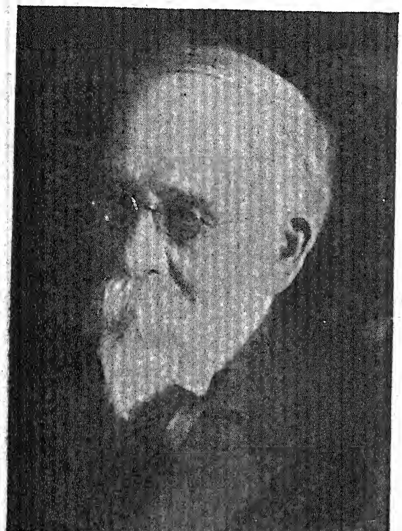


FIG. 103.—Charles E. Bessey (1845–1915). His life work at the University of Nebraska profoundly influenced the trend of botany in the United States. He was author of the first important American textbook of general botany and founder of a great phylogenetic system of plant classification. (*Courtesy of Raymond J. Pool.*)

The value of this work, considered as a whole, lies in its broad treatment of the entire plant kingdom, its excellent illustrations, and its phylogenetic arrangement of many groups. Being prepared by many authors, it is not surprising that it lacks somewhat in uniformity of treatment. Also in some groups, especially among the lower plants, phylogeny has been sacrificed for the convenience obtained by artificial grouping. This system now dominates the field of systematic botany, though not to the exclusion of all others.

Charles E. Bessey.—For the most part, American systematic botanists have given their attention to the collection and identification of plants, naming new species, herbarium making, and the writing of manuals to cover the vegetation of different parts of the country. With one notable exception they have not made extensive contributions to the development of taxonomic systems, this work having been done chiefly by Europeans. This exception was Charles E. Bessey, who received a part of his training under Asa Gray. A great teacher and investigator, he did his last and best work at the University of Nebraska.

In 1894, he submitted a system of classification that was a

modification of that of Bentham and Hooker, separating the gymnosperms from the angiosperms and reorganizing and rearranging a few orders of the latter.

Bessey gave much attention to the problem of determining the morphological indications of primitive versus advanced conditions in vegetative and reproductive structures and proposed many of the "morphological indicators of relationships" set forth in Chap. X of this book. His final[1] work was published in outline form shortly after his death[2] in 1915. It carried the classification only to the families, of which there were 300, subdivision into genera not being carried out. A condensation of it is as follows:

PHYLUM ANTHOPHYTA. **Flowering Plants**

CLASS ALTERNIFOLIAE (MONOCOTYLEDONEAE)

Subclass ALTERNIFOLIAE-STROBILOIDEAE
Order ALISMATALES
Alismataceae and 8 other families
Order LILIALES
Liliaceae and 12 other families
Order ARALES
Araceae and 2 other families
Order PALMALES
Palmaceae only
Order GRAMINALES
Poaceae and 4 other families
Subclass ALTERNIFOLIAE-COTYLOIDEAE
Order HYDRALES
Vallisneriaceae only
Order IRIDALES
Iridaceae and 10 other families
Order ORCHIDALES
Orchidaceae and 1 other family

CLASS OPPOSITIFOLIAE (DICOTYLEDONEAE)

Subclass OPPOSITIFOLIAE-STROBILOIDEAE
Order RANALES
Ranunculaceae and 23 other families
Order MALVALES
Malvaceae and 11 other families

[1] BESSEY, CHARLES E , The Phylogenetic Taxonomy of Flowering Plants, *Ann. Mo. Bot. Gard.*, **2**: 108–164, 1915.

[2] The main skeleton of the Bessey system was published much earlier (*Bot. Gaz.*, **24**: 145–178, 1897) but was revised from time to time with respect to certain details.

Order Sarraceniales
Sarraceniaceae and 1 other family
Order Geraniales
Geraniaceae and 21 other families
Order Guttiferales
Violaceae and 19 other families
Order Rhoedales
Brassicaceae and 6 other families
Order Caryophyllales
Salicaceae and 16 other families
Order Ebenales
Ebenaceae and 4 other families
Order Ericales
Ericaceae and 5 other families
Order Primulales
Primulaceae and 4 other families
Order Gentianales
Gentianaceae and 5 other families
Order Polymoniales
Solanaceae and 5 other families
Order Scrophulariales
Scrophulariaceae and 9 other families
Order Lamiales
Lamiaceae and 3 other families
Subclass Oppositifoliae-cotyloideae
Order Rosales
Rosaceae and 22 other families
Order Myrtales
Oenotheraceae and 14 other families
Order Loasales
Cucurbitaceae and 4 other families
Order Cactales
Cactaceae only
Order Celastrales
Vitaceae and 23 other families
Order Sapindales
Juglandaceae and 14 other families
Order Umbellales
Apiaceae and 2 other families
Order Rubiales
Rubiaceae and 4 other families
Order Campanulales
Campanulaceae and 3 other families
Order Asterales
Helianthaceae and 13 other families

For some families Bessey used names different from those under which they are commonly known; *e.g.*, Poaceae for Gramineae,

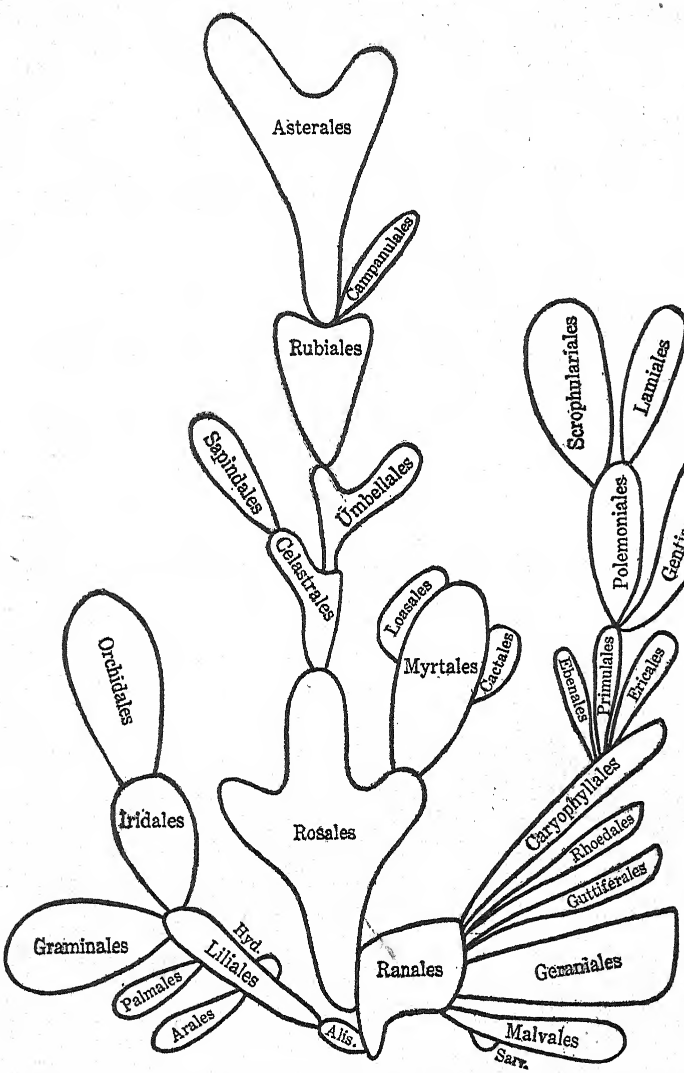


FIG. 104.—Bessey's conception of the relationships of the orders of angiosperms. Relationship is indicated by position. The areas are approximately proportional to the number of species in the orders. (*Redrawn after Bessey.*)

Brassicaceae for Cruciferae, and Lamiaceae for Labiatae. He also split some families into smaller families to a greater extent than is commonly done—*e.g.*, making Compositae an order (Asterales) with 14 families.

The arrangement of the orders to show phylogenetic relationships is give in Fig. 104. While in his publication he listed the monocotyledons before the dicotyledons, it must not be inferred that this is to indicate that they are the more primitive, for he definitely stated and shows in Fig. 104 his belief that the dicotyledons appeared first and that the monocotyledons branched off from them at a very early stage of their development.

COMPARISON OF THE SYSTEMS OF ENGLER AND BESSEY

Since the taxonomic systems of Engler and Bessey show the greatest divergence of any of those that have received the support of prominent botanists of recent years, and yet both have great merit, it seems well to summarize their differences.

Origin.—The two series of progressively improving taxonomic systems leading to those of Engler and of Bessey are given below:

John Ray (1686–1704)	John Ray (1686–1704)
Jussieu (1789)	Jussieu (1789)
Candolle (1819)	Candolle (1819)
Endlicher (1836–1840)	
Eichler (1883)	Bentham and Hooker (1862–1883)
Engler (1887–1909)	Bessey (1915)

Fundamental Conceptions.—Engler built his system of classification of the angiosperms in harmony with his ideas of phylogeny, which probably was, in most respects, correct; but many American taxonomists and some in other countries feel that the dicta of Bessey (see "Morphological Indicators of Phylogeny," page 276) are for the most part correct, and that his system built largely on them is a more natural one.

It is pretty generally agreed that flowers have been evolved from the strobili of pteridophytes, but we have no complete set of transitional forms either among living plants or among fossils. The most suggestive fossils are those of the extinct order of gymnosperms, the Bennettitales, which had reproductive structures somewhat like the flowers of our angiosperms. We can therefore only speculate on the steps by which flowers have evolved.

The two systems have many things in common, but there are some very important differences.

1. Engler considered the monocotyledons primitive and the dicotyledons derived from them, while Bessey held that the reverse was true.

2. Engler gave greater significance than Bessey to the union of petals (sympetaly), while Bessey gave greater significance to the floral axis, epigyny versus hypogyny.

3. It is generally conceded that flowers evolved from the strobili of gymnosperms. Engler's conception was that the ancestral strobilus was unisexual, producing either microspores or megaspores but not both, and that its morphological equivalent is the ament, each scale of the strobilus having become a unisexual,

FIG. 105.—Two conceptions of the evolution of the flower from the strobilus. In the center is a strobilus. According to Engler this contained only megaspores or microspores, and the entire strobilus developed into an ament, pistillate or staminate, each flower being apetalous and derived from a sporophyll of the ament. According to Bessey the strobilus contained megaspores below and microspores above and developed into a single flower, the lower sporophylls becoming sterilized and forming sepals and petals, those next above forming stamens, and the upper ones forming carpels. The axis shortened and became the strobiloid receptacle.

apetalous flower from which bisexual flowers and petaled flowers were later evolved. Bessey's conception is that the ancestral strobilus was bisexual with both microspores and megaspores, and that its morphological equivalent is a single bisexual flower like a buttercup. In the process of change the lower scales of the strobilus ceased to produce spores and became sepals and petals, those just above them evolved into stamens, and the upper ones evolved into carpels. Meanwhile, the axis of the strobilus to which the scales were attached shortened to form the receptacle. If it shortened only to a condition in which the top was convex or

flat, the receptacle was "strobiloid," and the flower was hypogynous. If it was depressed still farther so that the top of the receptacle was concave, the receptacle was "cotyloid," and the flower was perigynous or epigynous. It was natural, therefore, that Bessey should have given a higher value to the distinction between hypogyny and epigyny than did Engler, who had no such explanation for these differences in the floral axis.

4. Bessey further considered the apetalous flower as an advanced type in which the petals had been lost by reduction and called attention to their presence as vestigial scales in some apetalous flowers, whereas Engler treated apetalous flowers as primitive and ancestral to flowers with petals.

The Hallier System.—In 1905, Hans Hallier took issue with "Die natürlichen Pflanzenfamilien": (1) in giving a different origin to different members of the angiosperms, (2) in regarding the "Amentaceae" as primitive types, and (3) in the derivation of the monocotyledons. He proposed tentatively a phylogenetic system correcting these faults. In condensed form it is as follows:

A. SPOROPHYTES
- I Filicales
- II. Lycopodiales
  - *a.* Isosporae
  - *b.* Heterosporae
- II. Equisetales

B. SPERMATOPHYTES
- *a.* Gymnosperms (excluding Gnetaceae).
  - 1. Cycadaceae. 2. Bennettitaceae. 3. Coniferae
- *b.* Angiosperms
  - (*A*) Dicotyledons
    - I. Polycarpicae (Magnolineae, etc.)
    - II. Ranales (Nymphaeaceae, Ranunculaceae, etc.)
    - III. Rhoeadales (Capparidaceae, Cruciferae, etc.)
    - IV. Piperales (Piperaceae, etc.)
    - V. Malvales (Malvaceae, Urticaceae, etc.)
    - VI. Ebenales (Convolvulaceae, etc.)
    - VII. Geraniales (Geraniaceae, etc.)
    - VIII. Myrtiflorae (Myrtaceae, etc.)
    - IX. Rosales (Rosaceae, Leguminosae, etc.)
    - X. Ericales (Ericaceae, Primulaceae, etc.)
    - XI. Sarraceniales (Sarraceniaceae, etc.)
    - XII. Santalales (Santalaceae, Gnetaceae, etc.)
    - XIII. Umbelliflorae (Cornaceae, Umbelliferae, etc.)

XIV. Amentiflorae (Salicaceae, Juglandaceae, etc.)
XV. Passiflorales (Onagraceae, Campanulaceae, Compositae, etc.)
XVI. Centrospermae (Portulacaceae, Polygonaceae, etc)
XVII. Caprifoliales (Caprifoliaceae, etc.)
XVIII. Tubiflorae (Labiatae, Solanaceae, etc.)
(*B*) Monocotyledons (descendants of Nymphacaceae)
XIX. Helobiae (Alismaceae, Juncaginaceae)

(The work on the monocotyledons unfinished)

It will be noted that the Hallier system was developed simultaneously with that of Bessey and has many features in common with it.

The Work of Wettstein.—In 1901, Richard Wettstein published the first edition of his "Handbuch der systematischen Botanik." In the third edition (1924) a book of 1,000 pages covers the entire plant kingdom. The dicotyledons are regarded as polyphyletic and placed before the monocotyledons. Also, the lilies are considered more primitive than the grasses, which is a departure from the Engler and Prantl system. Wettstein considered the apetalous, amentiferous, woody plants to be more primitive than the Ranales (Magnoliaceae, Ranunculaceae, etc.) because fossils of the former have been found in older strata. It is agreed, however, that we have no fossil representatives of the most primitive flowering plants, so that paleontological evidence as to the antiquity of different groups of this class is not very conclusive.

The fourth edition, completed in 1935 after Wettstein's death, does not make any radical change in the system.

The Hutchinson System.—A more recent effort in this field is "The Families of Flowering Plants," by J. Hutchinson of the Royal Botanic Gardens, Kew, England; the first volume, on the dicotyledons, appeared in 1926; the second, on monocotyledons, in 1934. In its underlying principles it is much more like the Besseyan system than the Englerian system, but it differs considerably from both. Its main features are as follows:

1. It renews the ancient emphasis on the distinction between arborescent and herbaceous habit, but this character is here used in conjunction with other qualities. As a result of giving major emphasis to this distinction, two primitive or basal orders are recognized, the Magnoliales, mostly woody and giving rise to other orders that are mostly woody, and the Ranales, mostly

herbaceous and giving rise to other orders that are mostly herbaceous.

2. Partly as a result of the distinction just mentioned in the first feature, certain groups containing both woody and herbaceous members are made to appear polyphyletic, *i.e.*, some members arising from one ancestry and others from a different one. Such a position is given to the "Apetalae," the Urticales, the Umbelliflorae, and the Asterales, for example. Plants with apetalous flowers of course have no status as a phylogenetic group, but the status of the others is debatable. Whenever it can be established that different members of a group have separate ancestry, the group should be divided and the parts given distinct names, if the interests of phylogenetic taxonomy are to be served. Otherwise, a reticulate arrangement is formed.

3. In the monocotyledons the floral axis is given less significance than Bessey would give it, thus rearranging the genera of Liliaceae and Amaryllidaceae.

On the whole, the arrangement follows that of Bentham and Hooker. Even though some may doubt the wisdom of maintaining his distinctions between the various types of woody and herbaceous plants, all will agree that the system shows an advanced step in phylogenetic conception.

Summarizing the work of the last half-century, we find two different tendencies: (1) the work of Eichler and Engler, placing monocotyledons before dicotyledons, deriving dicotyledons from gymnosperms with unisexual strobili, and giving Amentiferae a primitive position among dicotyledons; (2) the work of Bessey, Hallier, Hutchinson, and Mez, giving monocotyledons an early derivation from the dicotyledons, deriving dicotyledons from gymnosperms with bisexual strobili, regarding Amentiferae as a heterogeneous group simplified by reduction, and making Ranales, in the older sense of the term, the basal group of the dicotyledons. The botanists of this group, while agreeing on these large issues, hold different views on the relationships of various orders and families and, it should be added, are quite in harmony with Engler on very many points.

COMPETITION OF SYSTEMS

It is regrettable that the systematic botanists of today are not in complete accord on taxonomic usage. All the systems in use at

the present time agree in many particulars but differ in others. Some of them cover the entire plant kingdom, while others deal only with limited groups, such as the bacteria, the fungi, or the higher plants.

Reasons for Lack of Accord.—There are at least five reasons for existing differences in taxonomic usage.

1. Often phylogenetic relationships are difficult to determine, the existing evidences being very meager. Under these circumstances the superficial mind may reach a very definite conclusion on evidence that is far from proof, the keen progressive mind may tentatively accept the evidence and make use of it until new evidence is found, while the slow or conservative mind will not use it at all. Then, again, certain lines of evidence may point to one relationship while other lines point to another. Under these circumstances the progressives may be divided into two groups.

2. Even though the evidences conclusively establish certain relationships, the resulting classification may not be used because there is an artificial grouping that is more convenient. Let us suppose, for example, that the Zygomycetes, the Oomycetes, the Ascomycetes, and the Basidiomycetes were known to have originated at different times from as many different groups of algae, and that the exact lines of descent were established. Even under these circumstances there is no doubt that some botanists would still treat the algae as one group, implying relationship, and the fungi as another. Or, again, even though some of the newer conceptions such as those of Bessey, Hallier, Hutchinson, and Mez are admittedly more in harmony with the evidences of phylogeny than are the older ones of Engler, the Engler and Prantl system would nevertheless continue in general use because of its accessibility, because of a desire for uniformity in practice, or because it is easier to continue it than to change.

It is indeed a criticism of some taxonomic specialists that they are content to use artificial groupings for plants rather than let phylogenetic consideration disturb their complacency.

3. Some confusion exists with regard to the names that should be applied to certain well-recognized groups. For example, among the family names we have Gramineae versus Poaceae, Leguminosae versus Papilionaceae versus Fabaceae, Cruciferae versus Brassicaceae, Umbelliferae versus Ammiaceae, and Compositae versus Carduaceae. Some of these are strict synonyms;

others vary somewhat in their generic inclusions. There are two principles (sometimes conflicting) that determine which synonym should be used. One is that a name of almost universal acceptance should not be replaced by an obscure one. The other is that the first valid name used for a group should not be replaced by another. Because some follow one of these principles and others follow the other, we have inevitable disagreement.

4. Since categories are not hard and fast entities, but only man-made devices for dealing with plants collectively, it is natural that some systematists would give a higher rating than others to certain groups. Some authorities consider Pomaceae and Drupaceae as families; others, as tribes of Rosaceae. Numerous other examples could be cited, and this is, in fact, one of the greatest forms of disagreement.

5. When a botanist has committed himself to a system of classification to the point of publishing it, he is likely to become unreceptive to evidence that would overthrow or greatly alter it. Criticism only makes him defend his ground more stubbornly, and he loses his attitude of open-mindedness. He and his opponents forthwith lead opposing schools of thought.

For the sake of expediency a teacher may be forced to give his students a system of classification that he does not consider the best from the standpoint of phylogeny, because the available manuals and the general practice of the region make such a policy necessary to avoid hopeless confusion. It is thus probable that the Engler and Prantl system is followed by many who, though appreciating its virtues, also recognize some of its faults and see ways of correcting them.

Organization of Herbaria.—Taxonomic classification expresses itself not only in publications but in herbaria. The herbaria found in most universities and some other institutions, such as the U.S. Department of Agriculture, are very large, some containing hundreds of thousands of specimens. These must be arranged in orderly fashion for convenience in the use of the herbarium. Most of them, the world over, are arranged according to the Englerian system.

PRESENT STATUS OF ANGIOSPERM CLASSIFICATION

It must not be supposed that the last word has been said on the phylogeny of the angiosperms, for researches carried on since the

time of Engler and Bessey indicate, as would naturally be expected, that neither one was able to picture natural classification correctly in all parts of his taxonomic system, and improvements must be expected for years to come. The Englerian system is being used in most manuals of botany because of the detailed presentation it has been given in Engler and Prantl's "Die natürlichen Pflanzenfamilien," a work of twenty-three large volumes with many illustrations, in contrast with Bessey's system, which was published in brief outline form, carrying the classification only to the family. Many botanists, however, especially those in America, agree with Bessey (1) that the dicotyledons are more primitive than the monocotyledons; (2) that the dicotyledons are a natural, monophyletic group; (3) that the Ranales are primitive while the Amentiferae are neither a primitive nor a natural homogeneous group; and (4) that apetalous flowers are not to be regarded as primitive because they failed to evolve petals but were derived from flowers with petals that have been lost through regressive development.

Need for Revision.—Differences of opinion concerning phylogenetic arrangement are natural and inevitable in the present state of our knowledge, and a shifting of ground must be expected as long as new evidence is forthcoming. It would be absurd for a botanical congress to seek to establish the facts by passing resolutions in favor of one system or another. Facts cannot be altered by proclamation. The writers of general treatises, however, can well lead the way by adopting the newer conceptions whenever they appear to be well established.

Present Tendencies.—We have reached a stage where the most progressive systematists are content with nothing short of phylogenetic arrangements for all groups of plants, although some feel that so complete an accomplishment can never be realized. Any other plan is looked upon as artificial and temporary, or merely an unscientific convenience—an expedient for some special purpose. In certain parts of the plant kingdom the relationships are fairly well understood. Some excellent work has already been published revising the detailed arrangement of some of the small groups—certain families, genera, etc. The phylogeny of each group needs to be studied not only for its own sake but in the hope of getting more light on the relationships of some of the other perplexing groups.

Researches in the Taxonomic Field.—The general adoption of the Englerian system in books and in herbaria has helped to stabilize taxonomic classification, but modifications and improvements must be expected in those groups where the work has been faulty. To the very extensive studies that have been made for centuries in the field of gross morphology new lines of evidence are now being added. The most fruitful of these are (1) paleobotany, (2) comparative anatomy, especially of the fibrovascular systems, (3) ecology and plant geography, (4) genetics, and (5) plant physiology, including "serum diagnosis."

CHAPTER XII

THE LITERATURE OF SYSTEMATIC BOTANY

Publications dealing directly or indirectly with the systematic aspect of botanical science have always held a conspicuous place in botanical literature; indeed, a mere list of titles would consume hundreds of pages. To keep the size of this chapter down to proper proportions relative to the rest of the book, the student will be given here but a few representative examples of different phases of the subject, especially since much of the literature is hardly within the grasp of the beginner but belongs in an advanced course. The following table of contents of this chapter will aid in finding any book that is cited here:

MEDIA FOR TAXONOMIC PUBLICATION

The earliest botanical works were written before the invention of the printing press and took the form of manuscripts, often bound in book form. Some of the most important of these have since been copied either as facsimile impressions or by printing, with or without translation.

In recent years taxonomic publication has taken varied forms—research articles, monographs, general treatises, manuals, etc. As for American journals, the *Bulletin of the Torrey Botanical Club* was formerly given over quite largely to taxonomic work, but in

recent years it has become more general. Those that are now devoted especially to this field are *American Midland Naturalist, Rhodora, Annals of the Missouri Botanical Garden, Journal of the Arnold Arboretum, Brittonia, Phytologia, Madroño, Darwiniana, Lloa. Lloydia, American Fern Journal, and Castanea.*

From the standpoint of establishing priority in the publication of names and descriptions of groups, all botanical works—journals, books, bulletins, etc.—in regular circulation are given equal recognition, and, indeed, priority can be established through works not strictly botanical, although their use is unfortunate, since articles they contain may easily be overlooked by those most interested in them. To discourage the publication of descriptions of species and other groups in obscure places, and especially in languages that are little used, recent rules have prescribed that a Latin diagnosis must be given in order to establish priority of publication.

THE EARLY CLASSICS

In the older literature a few works stand out as remarkable productions for the period in which they were written. Most of these have profoundly influenced the development of the science.

Enquiry into Plants.—Written by Theophrastus in nine books. Translated into English by Sir Arthur Hort in 1916; Loeb Classical Library, Harvard University Press. Published in two volumes with the Greek text and the English translation on opposite pages, giving a total of 908 pages.

This is the most important of the botanical writings of Theophrastus and the oldest botanical work of value existing today. It contains much real botanical information mixed with speculative philosophy and expresses freely the beliefs of the times, although in many cases the author casts doubt upon the superstitious ideas that he records.

De Re Rustica.—Written by Marcus Porcius Cato more than a century before Christ and printed in 1494; Loeb Classical Library, Harvard University Press, 1934. The book is devoted largely to agricultural and horticultural practices, methods of propagation, culture, varieties, etc., but plants are quite generally designated binomially, and many of these names are still in use. Said to be the oldest botanical work written in Latin.

Prodromus Systematis Naturalis Regni-Vegetabilis.—By A. P. de Candolle, University of Geneva, and others. Seventeen volumes and four index volumes, 1824–1873; published by G. Masson, Paris. This extensive work, by far the greatest treatise of its day on systematic botany, attempted to describe all known plants and arrange them according to the natural system of de Candolle.[1] After the death of this great botanist in 1841, the work was continued for more than 30 years by his associates.

Genera Plantarum.—By Carolus Linnaeus, Upsala University. Fifth edition, 1754, 500 pages, unillustrated. This edition is official in establishing the limit of priority for generic names. It describes 1,105 genera of plants of all kinds, citing the authority for the name in most cases. In general, the generic descriptions of the seed-bearing plants are restricted to the flower, fruit, and seed, ignoring vegetative portions.

Species Plantarum.—By Carolus Linnaeus, Upsala University. First edition, 1753, two volumes, 1,200 pages, unillustrated; facsimile edition, W. Junk, Berlin. In this, the most used of the early botanical classics, Linnaeus assembled under their genera practically all the species described up to that time, using very largely the binomial system but indicating varieties in some cases. Generic descriptions were not included. The work was partly the result of his own observations and partly compilation. A few previously published descriptions were overlooked, but the "Species Plantarum" was such a landmark in nomenclatural development that it was adopted as a starting point for priority in botanical names.

FUNDAMENTAL PRINCIPLES—MORPHOLOGICAL

The orderly taxonomic work of today is based on many principles that are the results of much painstaking research. Some of these have been known so long that their origin is obscure; others represent bold advances taken in recent times. The older works deal mostly with gross morphology and organization into categories, the newer ones with the findings of cytology, genetics, ecology, and plant geography.

The Phylogenetic Taxonomy of Flowering Plants.—By Charles E. Bessey, University of Nebraska, *Ann. Mo. Bot. Gard.*, **2,** 1915,

[1] "Théorie Elementaire de la Botanique," 1st ed., 1813; 2d ed., 1918.

155 pages, illustrated by one figure showing graphically the author's ideas of the relationships of the angiosperms. He sets forth many principles of taxonomy and from these constructs a phylogenetic system of classification of the angiosperms. His principles and system have steadily gained favor, although they have been found open to improvement. This represents the only attempt of an American botanist to construct a system of classification, and it is very meritorious.

Descriptive Systematic Botany.—By A. S. Hitchcock, U.S. Department of Agriculture. First edition, 1925, 216 pages, unillustrated; John Wiley & Sons, Inc. An excellent reference book on many topics relating to collecting, identifying, and the scientific arrangement of plants. The different codes of nomenclature that had been proposed up to that date are presented in comparison.

The Generic Concept in the Classification of Flowering Plants. By B. L. Robinson, Harvard University, *Science*, **23**: 81–92, 1906. The author here sets forth ideas regarding the correct delineation of genera and seeks to discourage the making of new genera on insufficient grounds.

Aspects of the Species Question.—By C. E. Bessey, N. L. Britton, J. C. Arthur, D. T. MacDougal, F. E. Clements, and H. C. Cowles, *Amer. Nat.*, **42**: 218–281, 1908. A symposium giving a masterful presentation of the best American ideas on the species concept and especially on the problem of finely divided species or subspecies. Later concepts have since been proposed.

The Concept of the Genus.—A symposium by Harley Harris Bartlett, Edgar Anderson, J. M. Greenman, Earl Edward Sherff, and W. H. Camp, *Bul. Torrey Bot. Club*, **67**: 349–389, 1940. The subject is presented by experienced taxonomists from several viewpoints, but that of the experimental approach of geneticists and ecologists receives only passing mention.

Mass Collection.—By Edgar Anderson, Ralph O. Erickson, and Norman O. Fassett, *Ann. Mo. Bot. Gard.*, **28**: 287–374, 1941. This series of papers explains that for research purposes samples of significant parts taken from a considerable number of individuals of a plant population in a given locality, representing a species, subspecies, variety, or race, have great advantages over single specimens taken in the usual way. Methods are given for sampling, preserving, and using such mass collections.

Origin of Species.—By Charles Darwin. First edition, 1859; sixth edition, 1893. Two volumes, 365 and 339 pages, respectively; bound together unillustrated; D. Appleton-Century Company, Inc., New York. This book, preceded by the brief expositions of Wallace and Darwin on the same subject a year earlier, constitutes the first adequate presentation of the theory of the evolutionary origin of living things. It is written in the style of a research publication, referring to previous statements by others, submitting evidences, and drawing conclusions. It is the forerunner of a long series of works on evolution by Darwin and numerous other writers.

Evolution by Means of Hybridization.—By J. P. Lotsy. First edition, 1916, 166 pages and 2 illustrations; Martinus Mjhoff, The Hague. A discussion well adapted to student use. The author dwells especially on the part played by conjugation in the formation of new species and varieties and thus paves the way for the modern genetic and ecological conceptions, *i.e.*, the "experimental method" of taxonomy.

What Evolution Is.—By George H. Parker, Harvard University. First edition, 1926, 173 pages and 4 pages of illustrations; Harvard University Press. A highly authoritative, dispassionate presentation of the history, evidences, and mechanism of evolution as it has been disclosed by more than half a century of investigation by many careful workers. The book is suited to students and general readers.

Evolution for John Doe.—By Ward Henshaw. First edition, 1925, 354 pages, illustrated; The Bobbs-Merrill Company. The author, a layman, has studied the subject from all angles and here presents a good, readable account of it that will appeal to other laymen.

Origin through Evolution.—By Nathan Fasten, Oregon State College. First edition, 1929, 456 pages, and 75 illustrations; Alfred A. Knopf, New York. This book gives, in readable form, a well-rounded account of the development of our ideas concerning organic evolution, with emphasis on the evidences bearing on the subject and the laws governing its operation.

FUNDAMENTAL PRINCIPLES—GENETIC, ETC.

For centuries plants were classified on the basis of their morphology and anatomy, and certain principles were evolved to

guide taxonomists in the interpretation of their observations. Some references to these principles are cited above. More recently other branches of botany—genetics, ecology, etc.—have added new lines of evidence based on both observation and experiment. Some of these are reviewed below.

Principles of Genetics.—By Edmund W. Sinnott and L. C. Dunn, Columbia University. Third edition, 1939, 408 pages and 147 illustrations; McGraw-Hill Book Company, Inc. This book serves admirably to give the genetic evidence concerning the methods by which evolution takes place in plants and animals.

The New Systematics.—Edited by Julian Huxley, England. First edition, 1940, 583 pages, illustrated; The Clarendon Press, Oxford, England. Twenty-two chapters, each written by a different author, who had specialized in the field covered and represented different nationalities. The book covers in a thorough and authoritative way the newer researches in ecology, plant geography, paleontology, genetics, and other fields that have a bearing on taxonomy and where possible correlates them with the older morphological findings and conclusions. It is the fullest exposition up to 1940 on the experimental method in taxonomy.

Genetics and the Origin of Species.—By Theodosius Dobzhansky, Columbia University. Second edition, 1941, 446 pages, illustrated; Columbia University Press. Although written by a zoologist, this book contains much illustrative material from the plant kingdom. The fundamental principles brought out in explanation of the mechanism of evolution are applicable to both animals and plants and represent the author's interpretation of the genetic researches in this field.

The Genotypical Response of the Plant Species to the Habitat. By Göte Turesson, Institute of Genetics, Askarp, Sweden, *Hereditas*, **3**: 211–350, 1922, illustrated. The work was based largely on transplants made from one environment of central and northern Europe to another. Studies were made on the anatomy, cytology, and gross morphology of the transplants and on the results of hybridization. Here are introduced the terms cenospecies, ecospecies, ecotypes, and ecophenes as categorical equivalents of genera, species, subspecies, and variants but in a different way, the latter being based on morphology and the former on genetic and ecological experiments.

The Concept of Species Based on Experiment.—By Jens Clausen, David D. Keck, and Wm. M. Hiesey, *Amer. Jour. Bot.*, **26**: 103–106, 1939. A concise presentation of the newer concept of species and other lower categories. In contrast with the older conceptions based on gross morphology, this newer conception is based on experimental work in which closely related plants are crossed and the resulting offspring (if any are produced) are studied under different environmental conditions, some plants being isolated and others given a chance to interbreed. Stability in the product under experimental conditions determines its category—species, subspecies, etc.

Experimental Studies on the Nature of Species.—By Jens Clausen, David D. Keck, and William M. Hiesey, Carnegie Institution of Washington at Stanford University, Publication No. 520, 1940. Part I, on "The Effect of Varied Environments on Western North American Plants," has 452 pages, illustrated. Continuing the work begun by the late Dr. Harvey Monroe Hall of the same institution, the authors have transplanted a considerable number of species of perennials into three dissimilar regions to test the effects on them of the wide range of ecological conditions—altitude, moisture, temperature, etc.—found in California. Some mention is made of chromosome numbers and other cytological data, but the work deals mostly with ecology in relation to taxonomy, the cytological and genetic aspects being treated in a companion volume now in preparation.

The Role of Isolating Mechanisms in the Differentiation of Plant Species.—By G. Ledyard Stebbins, Jr. *Biological Symposia*, **6**: 217–233, 1942. This is representative of the recent papers reporting the results of researches undertaken to show the necessity of isolation for the prevention of cross-fertilization, if species and other lower categories are to become established following hybridization. It also discusses the different kinds of isolating mechanisms and their origin. It has a valuable bibliography on the subject.

Chromosome Number and the Relationship of Species in the Genus Viola.—By Jens Clausen, *Ann. Bot.* [London], **41**: 677–714, 1927. Based on original investigations and on citations from other cytologists, the chromosome numbers of more than forty species of *Viola* are given. Fourteen different numbers, ranging from six to thirty-six, are given. In a phylogenetic study the

number, size, and shape of the chromosomes are compared with the morphological characters. Through crossing it was found that individuals sufficiently identical in morphology to be classed as the same species can be derived from unlike parentage. Some explanations are offered for partial and complete sterility in the offspring.

RULES OF BOTANICAL NOMENCLATURE

After Linnaeus had convinced the biological world that the binomial system of nomenclature was the best one to use, the naming of plants was extensively carried on by many botanists who were widely separated and working independently, and much confusion resulted. To secure greater uniformity in procedure the leading botanists of the world have held a number of international congresses and adopted rules of procedure. The rules that they adopted and that survived the action of later congresses are given below. Botanical nomenclature has become so complicated that a summary of the most important rules is given on pages 234 to 236 of this book.

Codes of Nomenclature and Botanical Congresses.—By Herbert C. Hanson, *Amer. Bot.*, **31:** 114–120, 1925. A brief review of the national and international botanical congresses up to 1910, with references to the publications of their proceedings, and codes of botanical nomenclature.

Laws of Botanical Nomenclature.—By Alphonse P. de Candolle, translated from the French by Dr. Weddell, *Amer. Jour. Sci.*, **96:** 63–77, 1868. This paper gives the so-called Paris Code in full, with editorial remarks.

International Rules of Botanical Nomenclature.—By John Briquet, Reporter General for the International Botanical Congress of Vienna, 1905, and Brussels, 1910. Second edition, 1912, unillustrated, Gustav Fischer, Jena. Written in three languages, French, English, and German, in one volume. The English section covers 19 pages and the entire work 110 pages, of which 29 are devoted to *nomina conservanda* in Latin, applicable to the three sections.

American Code of Botanical Nomenclature.—By the American Nomenclature Commission, *Bul. Torrey Bot. Club.*, **34:** 167–178, 1907, unillustrated. A brief statement of the reasons for advo-

cating the American Code as a substitute for the recently formulated International Rules, followed by the rules themselves.

Type-basis Code of Botanical Nomenclature.—By A. S. Hitchcock, U.S. Department of Agriculture, *Science*, **49**: 333–336, 1919, unillustrated. The author, as chairman of a committee of the Botanical Society of America on generic types, here makes a brief report for the committee and records the rules recommended for adoption and known as the Type-basis Code.

International Rules of Botanical Nomenclature.—By John Briquet and A. B. Rendle of the Committee for Nomenclature for the 1930 Botanical Congress of Cambridge, 1935, Gustav Fischer, Jena. Written in three languages, English, French, and German, in one volume. The English section covers 26 pages exclusive of the *nomina conservanda*, etc. (20 pages). This work consists of an amplification of earlier rules. It includes the type concept and introduces the term "epithet" for the name of the species when it stands alone without the generic name. It is the most nearly complete code of International Rules of Nomenclature thus far published, lacking only the amendments authorized at the 1935 Congress of Amsterdam.

Additions and Amendments to the International Rules of Botanical Nomenclature, Edition 3.—By twelve botanists, *Kew Roy. Bot. Gard. Bul. Misc. Inform.*, No. 21932, pages 65–92. This is virtually a supplement to the International Rules as adopted by the 1930 International Congress at Cambridge. It embodies the work of the 1935 Congress at Amsterdam and the recommendations of committees authorized by that congress. It consists of minor changes in the rules, corrections, and decisions concerning the names of certain groups that were controversial.

Conservation of Later Generic Homonyms.—By Alfred Rehder *et al.*, *Kew Roy. Bot. Gard. Bul. Misc. Inform.*, Nos. 6–9, 1935, pages 341–557. The subject matter is indicated in the title.

Additional Nomina Generica Conservanda (Pteridophyta and Phanerogamae).—By T. A. Sprague, *Kew Roy. Bot. Gard. Bul. Misc. Inform.* No. 3, 1940, pages 81–134. The subject matter is indicated in the title.

Principal Decisions Concerning Nomenclature Adopted by the Sixth Botanical Congress at Amsterdam.—By T. A. Sprague, *Jour. Bot.* [London], **74**, 1936. This paper gives some of the most

important work of the Amsterdam Congress in simpler form than the two publications cited above.

Terminology of Types.—By Donald Leslie Frizzell, *Amer. Midland Nat.*, **14**: 637–668, 1933. This paper gives a brief discussion of nomenclatural types of plants and animals, followed by an extensive list of the terms, both those in current use and others that are synonyms or obsolete, for the different kinds of types, with definitions. It has a good bibliography of previous papers on the subject.

Types of Species in Botanical Taxonomy.—By W. T. Swingle, *Science*, **37**: 864–867, 1913. A discussion of the significance of type specimens, the value and care of such specimens, and the methods of reproducing, or duplicating for distribution to other herbaria, the one real type specimen. It gives a brief classification of type materials, which is practically the same as that followed by botanists at the present time. It contains references to other papers on the same subject.

WORLD FLORAS AND TAXONOMIC SYSTEMS

A few great taxonomists have had the vision to construct systems of classification for great groups of plants, such as the Spermatophyta. Some of these have been published in skeleton form for the higher categories only; others have been carried down to the species. All but one of these taxonomic systems have been the products of European botanists. That of Charles E. Bessey is the work of an American and is based partly on the earlier publications of Europeans. All the systems now in use have had an evolutionary history and are not the product of any single botanist.

Genera Plantarum.—By G. Bentham and J. D. Hooker, Kew, England. First edition, 1862–1883, three volumes, 3,577 pages, unillustrated; published by Reeve & Co., London. This monumental work gives a fairly complete classification of the higher plants with a definite system of categories and descriptions of all groups. The sequence is dicotyledons, gymnosperms, and monocotyledons. This work dominated the field of systematic botany more than any other prior to "Die natürlichen Pflanzenfamilien," of Engler and Prantl. It used a system of categories somewhat different from that of today—cohort for order and order for

family. Many consider the sequence of families to be more natural than that of Engler and Prantl.

Die natürlichen Pflanzenfamilien.—By Adolph Engler, Berlin, and K. Prantl, Breslau. First edition, 1887–1909, second edition in preparation, eight volumes of which have been published to date. The largest work of its kind ever written, filling twenty-three volumes and occupying several feet of shelf space. Profusely illustrated; W. Engelmann, Leipzig. This great work covers the entire plant kingdom and is world-wide in its scope. It carries the classification to genera and in some cases to species, but there is considerable lack of uniformity in treatment owing to its composite authorship, many botanists having taken part in the preparation of the treatise. This publication has dominated the field of systematic botany since its publication. Most herbaria of the world and most botanical manuals follow its sequence of families. There is, however, at present a considerable breaking away from some of its phylogenetic conceptions.

Syllabus der Pflanzenfamilien.—By Adolph Engler and Ludwig Diele, University of Berlin. Eleventh edition, 1936, 419 pages and 476 illustrations; Gebrüder Bornträger, Berlin. This book is usually thought of as a condensation of "Die natürlichen Pflanzenfamilien." It consists of an introduction on principles of classification, a list of families and higher categories according to the Engler system, and a brief discussion of families and tribes.

Handbuch der Systematischen Botanik.—By Richard Wettstein, University of Wien. Fourth edition, 1933–1935, two volumes, 1,152 pages, 709 plates, and 3,974 figures; Franz Deuticke, Leipzig. The great value of this work lies in its modern and original conceptions and its excellent descriptions and illustrations.

The Classification of Flowering Plants.—By A. B. Rendle, British Museum. Volume I, Gymnosperms and Monocotyledons. First edition, 1904, 403 pages and 187 illustrations. Volume II, Dicotyledons. First edition, 1925, 636 pages and 279 illustrations; Cambridge University Press. This work makes no pretense of listing all species but gives remarkably fine descriptions of all the families, the morphological tendencies within the families, and the modifications of the family types. It is particularly strong in indicating the morphological equivalents of

highly specialized organs. Examples are drawn from the flora of the entire world.

The Families of Flowering Plants.—By J. Hutchinson, Royal Botanic Gardens, Kew, England. Volume I, Dicotyledons. First edition, 1926, 328 pages and 264 illustrations, with an elaborate diagram of phylogenetic arrangement. Volume II, Monocotyledons. First edition, 1934, 243 pages and 107 illustrations; Macmillan & Company, Ltd., London. Hutchinson's work represents the latest general exposition of the flowering plants. It is refreshing in its originality, with a number of progressive features: a statement of phylogenetic principles; a new phylogenetic scheme (reviewed on page 299) that is bound to provoke fruitful discussion; a grouping of the orders and families according to their characters, tendencies, and consequent affinities; an extensive key to families, world-wide in its scope; a concise and well-illustrated description of each family, accompanied in many instances by a distribution map.

Flowers and Flowering Plants.—By Raymond J. Pool, University of Nebraska. Second edition, 1941, 428 pages and 211 illustrations; McGraw-Hill Book Company, Inc. This book contains much of fundamental interest to students of systematic botany and to amateur botanists who would carry their studies beyond the mere naming of plants. It also presents in the most workable form the principles and system of classification set forth by C. E. Bessey. Emphasis is laid on a study of families, and more than 100 are described rather fully. These are beautifully illustrated, and nearly all are given their floral formulae according to the plan advocated by Clements (see page 40).

REGIONAL FLORAS AND MANUALS

For the convenience of those who wish to identify the flowering plants of their own region, many manuals on the local flora have been written. They make no pretense of including all known species but aim to be complete for a limited area, generally a state or a group of states. The size of the book is thus kept down, and it is much easier to find the name of any plant in question than it would be in a great world flora describing all known species. Some of these books, such as "Gray's Manual," have been revised and reprinted. Others serve their purpose for a time and go out

of print, to be replaced with others by different authors. Only a few of these will be listed here, for the publication by Blake and Atwood, given below, may be consulted for any desired region.

Geographical Guide to the Floras of the World.—By S. F. Blake and Alice C. Atwood, U.S. Department of Agriculture, Miscellaneous Publication No. 401; Government Printing

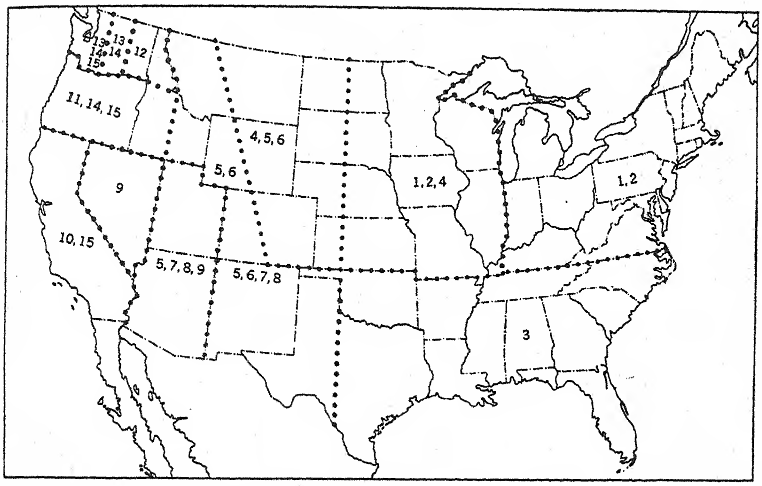


FIG. 106.—Range covered by the principal botanical manuals of the United States.

Key to Numbers on Map

1, Gray's "Manual of Botany." 2, Britton and Brown's "Illustrated Flora." 3, Small's "Flora of the Southeastern United States." 4, Rydberg's "Flora of the Prairies and Plains." 5, Rydberg's "Flora of the Rocky Mountains." 6, Coulter and Nelson's "Rocky Mountain Botany." 7, Wooten and Standley's "Flora of New Mexico." 8, Tidestrom and Kittell's "Flora of Arizona and New Mexico." 9, Tidestrom's "Flora of Utah and Nevada" 10, Jepson's "Flowering Plants of California." 11, Peck's "Flora of Oregon." 12, St. John's "Flora of Southeastern Washington and Adjacent Idaho." 13, Frye and Rigg's "Northwest Flora." 14, Helen Gilkey's "Handbook of Northwest Flowering Plants." 15, Abram's "Flora of the Pacific States."

Office, Washington, D.C., 1942. Part I lists the floras of Africa, Australia, North America, South America, and islands of the Atlantic, Pacific, and Indian oceans. The very large number of local floras cited is well arranged with annotations, followed by an author index and a regional index.

Gray's New Manual of Botany.—Earlier editions by Asa Gray, Harvard University. Seventh edition, 1908, revised by B. L. Robinson and M. L. Fernald, Harvard University, 926 pages and

1,036 illustrations; American Book Company. An eighth edition is in preparation. No work of its kind is better known or more used than "Gray's Manual." The analytical keys have been thoroughly tested and the descriptions are concise but clear. The illustrations, though small, are well chosen.

Flora of the Prairies and Plains of Central North America.—By P. A. Rydberg, New York Botanical Garden. First edition, 1932, 969 pages and 600 illustrations; published by the New York Botanical Garden. This flora covers the region from the Great Lakes to the foothills of the Rocky Mountains and south to Oklahoma. It consists of keys and descriptions similar to those of the Rocky Mountain flora by the same author but follows the International Rules of Nomenclature.

Flora of the Rocky Mountains and Adjacent Plains.—By P. A. Rydberg, New York Botanical Garden. First edition, 1917, 1,110 pages, unillustrated; published by the author. Rydberg's flora covers a somewhat wider range than Coulter and Nelson's manual and includes many more genera and species. The American Code of nomenclature is followed.

New Manual of Botany of the Central Rocky Mountains.—By John M. Coulter, University of Chicago, revised by Aven Nelson, University of Wyoming. Second edition, 1909, 646 pages, unillustrated; American Book Company. This book, of convenient classroom size, has proved a highly useful work for a large area of the country.

Manual of the Flowering Plants of California.—By Willis L. Jepson, University of California. First edition, 1925, 1,238 pages and 1,023 illustrations; published by the Associated Students Store, University of California. This book gives an admirable presentation of the flora of the southwestern part of the country. The species are well delineated and illustrated, and brief but valuable data are given on the ecology of the different zones and the habitat favorable to each species.

Flora of the Southeastern United States.—By J. K. Small, New York Botanical Garden, 1933, 1,554 pages, illustrated; published by the author. This work is indispensable for a study of the flora of the southeastern fourth of the United States and is admirably executed. The latest edition makes use of the International Rules of Nomenclature.

TAXONOMIC TREATMENT OF LIMITED GROUPS

A considerable number of books and papers have been written in restricted fields of taxonomy, sometimes taking the form of monographs of certain natural groups—genera, families, etc.—and sometimes presenting such miscellaneous groups as appeal to certain classes of readers—trees, flowers, edible plants, etc.

The Silva of North America.—By Charles S. Sargent, Arnold Arboretum, Harvard University. First edition, 1891–1902, fourteen volumes containing 2,185 pages and 740 splendid, full-page lithographic plates; Houghton Mifflin Company. Sargent's "Silva" is one of the finest pieces of work produced in this country. The trees are considered by families, with some attention to the interrelationships of genera and species. The synonymy of the specific names is given, with excellent descriptions of each species, and information on ecology and economic importance. The illustrations with their fine details are unsurpassed.

Manual of the Trees of North America.—By Charles S. Sargent, Arnold Arboretum, Harvard University. Second edition, 1922, 910 pages and 783 illustrations; Houghton Mifflin Company. Since its first appearance this work has been the standard condensed reference book on the trees and shrubs of this country. It describes both native and introduced species, following the Engler and Prantl arrangement and the International Rules of Nomenclature.

Manual of Trees and Shrubs Hardy in North America.—By Alfred Rehder, Arnold Arboretum, Harvard University. Second edition, 1940, 996 pages, unillustrated; The Macmillan Company. This book classifies and describes more than 2,300 species of woody plants with numerous varieties and hybrids and gives distribution zones and notes on adaptability.

Timbers of North America.—By Samuel J. Record, Yale University. First edition, 1934, 196 pages, illustrated; John Wiley & Sons, Inc. The strength of the book lies in its discussion of the anatomy and histology of the different kinds of woods. It contains a key of twenty-eight pages for the identification of woody species, based on general and microscopic characters of the wood, by which the species can be determined without regard to external morphology. It has good popular descriptions of more than seventy species, giving distribution, abundance, and economic uses.

Winter Botany.—By William Trelease, University of Illinois. Third edition, 1925, 438 pages and over 300 illustrations; published by the author. The book is of convenient pocket size, and, while semipopular, it is highly authoritative. It contains analytical keys and excellent descriptions of most of the trees, shrubs, and woody vines in their winter condition. It is excellent for the use of students and the better informed amateur botanists.

Northern Rocky Mountain Trees and Shrubs.—By J. E. Kirkwood, State University of Montana. First edition, 1930, 340 pages, 35 plates and 87 text figures, mostly original; Stanford University Press. In readable style and with scientific accuracy this book describes practically all the trees and other woody plants of the area covered, with information on the economic importance and points of peculiar interest applying to each. Keys are provided for classification into families, genera, and species.

Gymnosperms—Structure and Evolution.—By Charles Joseph Chamberlain, University of Chicago. First edition, 1935, 484 pages and 396 illustrations; University of Chicago Press. Each of the seven orders of gymnosperms is thoroughly discussed and illustrated, and especial attention is given to the phylogeny of each group. The book is highly authoritative and written in an interesting style.

Monocotyledons.—By Agnes Arber, Balfour Laboratory, Cambridge, England. First edition, 1925, 258 pages and 160 illustrations; Cambridge University Press. A well-rounded, thorough discussion of the morphology and affinities of the group. While the work is not primarily taxonomic, it contains much information upon which the taxonomy of this great group must be based. It is a fine example of this type of monograph.

Manual of the Grasses of the United States.—By A. S. Hitchcock, U.S. Department of Agriculture. First edition, 1935, 1,040 pages and 1,696 illustrations; Government Printing Office, Washington, D.C. An indispensable work to students of agrostology. It contains discussions of grass morphology and economic uses, keys, descriptions of species and other groups, and a very full glossary of the technical terms used in this field.

North American Cariceae.—By Kenneth Kent Mackenzie. First edition, 1940, two large volumes, 547 pages, profusely illustrated, with keys for identification in a separate pamphlet;

published by the New York Botanical Garden. The most nearly complete and satisfactory descriptions of the species of *Carex* that has yet been published. Distribution and habitats are included.

A Monograph of the Section Oreocarya of Cryptantha.—By Edwin Blake Payson, *Ann. Mo. Bot. Gard.* **14:** 211-347, 1927. This paper represents a thorough and well-balanced study of a subgenus. It includes morphological distinctions between this and related subgenera and between the included species, geographical distribution from a world standpoint, phylogeny and evolution, even approaching the "new systematics" that is receiving so much attention at the present time. It has a philosophic tone throughout.

Poisonous Plants of the United States.—By Walter Conrad Muencher. First edition, 1939, 266 pages, illustrated; The Macmillan Company. Following a fifteen-page introduction on different methods of classifying poisonous plants, those found in this country, of which there are about 400, are classified according to plant families. Under the discussion of each are given the scientific and common names, the description, the distribution and habitat, and statements concerning the poisonous principle and its effects.

The Phylogenetic Method in Taxonomy; The North American Species of Artemisia, Chrysothamnus, and Atriplex.—By Harvey M. Hall and Frederic E. Clements, The Carnegie Institution. First edition, 1923, 355 pages, 47 text figures and 58 plates. Publication No. 3564; Carnegie Institution of Washington, D.C. Following an introduction of thirty pages on general principles of taxonomy, the three genera mentioned in the title are discussed. The method of treatment of the three genera is similar. The characters or criteria used for subdivision are described, the affinities of the genera with related genera are discussed, and the internal relationships are shown by diagrams. Each genus is divided into sections, and these into species. What is more striking, each species has been studied with reference to its recognizable varieties, which are few in some species and many in others—the more plastic ones. These subspecies are designated trinomially. It is inevitable that where such fine subdivisions are recognized and expressed in phylogenetic diagrams there will be some differences of opinion among the critics, but these two workers have

indicated ideals that others could well follow in monographing generic and other groups.

CULTIVATED AND ECONOMIC PLANTS

Most descriptive manuals or floras of the different regions do not include introduced species that are under cultivation unless they have escaped and become established with the native flora. The identification and study of the cultivated plants have been facilitated by a few important works. It is quite impossible to keep books for the identification of all plants cultivated in America up-to-date for the reason that new species are constantly being originated and others are being introduced from abroad.

Origin of Cultivated Plants.—By A. P. de Candolle, Academy of Science of the Institute of France. First edition, 1882, 468 pages, unillustrated; D. Appleton-Century Company, Inc. Following a discussion of some thirty pages on the character of the evidence applicable to such a discussion, the author traces many varieties and species grown in different parts of the world back to ancestral forms growing wild. While considerable evidence has been brought out since the book was written concerning the origin of certain crop plants, most of the conclusions still hold.

Studies on the Origin of Cultivated Plants.—By N. Vavilov, Leningrad, *Bull.* 2 of Applied Botany and Plant-Breeding, **16,** 1926, 108 pages, 6 illustrations, and 7 distribution maps. This paper presents modern methods of determining the place of origin and ancestral forms from which cultivated plants have arisen. The older methods of comparing cultivated varieties with similar wild ones of the vicinity and of using archaeological records are not ignored, but to these are added what the author designates as the botanical method, which includes genetic and cytological evidence and lays especial stress on the hypothesis that around the point of origin of a species much minor variation will be found among the individual plants, while in other regions to which it has spread there is greater uniformity. Evidence is also shown that certain species once regarded as weeds were later domesticated.

Manual of Cultivated Plants.—By L. H. Bailey, Cornell University. First edition, 1924, 851 pages and 14 illustrations; The Macmillan Company. The book contains in compact from analytical keys and descriptions of most species and many vari-

eties of plants that are cultivated in the United States for use or pleasure. It is up-to-date in its taxonomy and nomenclature and gives some information concerning the origin of many of the forms treated.

Standard Cyclopedia of Horticulture.—By L. H. Bailey. Reissue of second edition, 1935, three volumes, 3,639 pages, profusely illustrated; The Macmillan Company. A classification and descriptions of the cultivated plants of the United States and Canada, with information concerning their culture and use.

Hortus Second.—By L. H. Bailey and Ethel Zoe Bailey. Second edition, 1941, 778 pages, illustrated; The Macmillan Company. A handy reference to the cultivated plants of America, giving names and descriptions and concise information on their use.

Standardized Plant Names.—By Harlan P. Kelsey and William A. Dayton. Second edition, 1942, 675 pages; published by J. Horace McFarland Company for the American Joint Committee on Horticultural Nomenclature. This book lists more than 90,000 names of economic plants and plant products. The botanical and common names are given, accompanied by lists of cultivated varieties. More than 8,000 new common names have been added, and efforts have been made to reduce confusion due to use of the same common name for different species.

Herbals, Their Origin and Evolution.—By Agnes Arber. Second edition, 1938, 326 pages, illustrated; The Macmillan Company. An historical account of the development and use of drug plants from 1470 to 1670.

Plants Useful to Man.—By W. W. Robbins, University of California, and Francis Ramaley, University of Colorado. Second edition, 1937, 422 pages and 235 illustrations; The Blakiston Company. In very readable style the authors present the origin, distribution, culture, and uses of the most important economic plants of the United States and many others grown in the tropics and elsewhere. For the most part the plants are grouped according to natural families.

Range Plant Handbook.—By the Forest Service of the U.S. Department of Agriculture. First edition, about 700 pages, illustrated; Government Printing Office, Washington, D.C., 1937. A large number of grasses and other range plants are described in nontechnical terms and illustrated. Both botanical and common names are given. There are discussions of groups

and individual species giving information concerning their range, abundance, and value.

NONTECHNICAL FLORAS

The phase of botany that most appeals to the amateur is the recognition and naming of the wild flora. Few amateurs give attention to any other branch of botany, while thousands seek to learn the names of at least the most conspicuous plants. Some amateur systematists take up the subject in the most superficial way, being content with almost any common name that they learn by word of mouth and never really examining plants at all, while others become remarkably proficient in all but the most difficult groups.

To aid the worthy attempts of those who seek to learn the names of the wild plants for their own pleasure a considerable number of books have been written. Such a task is by no means easy, and most such books have not been very successful. Various devices have been employed to aid the layman in identification work. General descriptions alone are almost total failures. Technical descriptions discourage all but the most determined. Semipopular keys are quite valuable to the more studious amateurs and lead naturally to semipopular descriptions which are sufficient for species that are clear-cut and few in a genus. Illustrations are being more and more used and are valuable to supplement keys and descriptions. They have some weaknesses. Good illustrations are so expensive that only a small percentage of the species can be honored by them. Furthermore, many species are so much alike in general appearance that a given picture may apply equally well to several of them. There is no convenient way of associating the plant in question with its picture in a profusely illustrated work except by keys; hence the superficial worker spends much time rambling through the book hunting for the desired illustration, which may not be there at all. There is no easy road to success in identifying plants, and all who expect to become proficient must master the morphology and terminology required to use technical manuals. It has been observed that the amateur who has not the courage to learn generic and specific botanical names lacks also the persistence required to identify plants.

To simplify the work of identification, popular floras are usually

restricted geographically and treat only the more conspicuous species; hence many plants will be collected that have been omitted from the book.

Field Book of American Wild Flowers.—By F. Schuyler Mathews. Revised edition, 1912, 587 pages, 24 colored plates, and more than 300 line drawings; G. P. Putnam's Sons. For the eastern half of the United States this book serves as a good guide for the amateur. The plants are arranged by families, and most of the prominent species are described and illustrated. Two keys facilitate the association of the specimen with its description: a color key, and a key based on the more obvious morphological characters. Both common and botanical names are given, the latter following the International Rules.

Rocky Mountain Flowers.—By F. E. Clements and Edith S. Clements. Third edition, 1928, 390 pages and 47 plates, more than half of which are colored; The H. W. Wilson Company, New York. The presentation is semipopular, with numerous keys and fine illustrations. Families and genera are described, and some of the species are listed but not described. The distinctive feature of the work is a flower chart that aids in the location of families by lines and formulae that indicate different types of floral structure. Some skill is required to use this chart but it is very helpful when mastered.

Wild Flowers of the North American Mountains.—By Julia Henshaw, Alpine Club of Canada. First edition, 1915, 383 pages and 83 plates, a fourth of which are colored; Robert M. McBride & Company, New York. The book is particularly applicable to Canada and the northern United States. The key is not of an analytical type, being merely a synopsis, but as a device for aiding the reader in placing his specimen the plants are grouped according to flower colors, a method that in most cases narrows the search down to a point where the desired picture can be found with some readiness. The illustrations are excellent and both technical and popular descriptions are given, with a liberal admixture of sentiment.

Wild Flowers.—By Homer D. House. Imperial edition, 1936, 362 pages and 264 full-page colored illustrations; The Macmillan Company. An interesting three-page introduction is followed by twenty-three pages of descriptive matter and definitions applying to flowering plants, which aid in the use of the keys

to the species. The plants are arranged by families from monocotyledons to Compositae.

American Plant Names.—By Willard N. Clute. Third edition, 1940, 285 pages with supplement; published by the author at Indianapolis, Indiana. A list of the scientific names of the wild plants of the northeastern quarter of the United States but somewhat applicable to a wider range. For each species the corresponding common names are given.

PALEOBOTANY

Paleobotany holds the joint interest of geologists, botanists, and zoologists because of its record of conditions on the earth during past ages. Not only does it shed much light on the phylogenetic relationships of plants, but it indicates in many cases the climatic and other environmental conditions under which the development of the plant and animal kingdoms, including man, took place.

Studies in Fossil Botany.—By D. H. Scott, Royal Botanic Gardens, Kew, England. Third edition, 1920, two volumes containing 880 pages and 326 illustrations; A. & C. Black, Ltd., London. Volume I covers the pteridophytes and lower plants and Volume II the higher plants. We have here an authoritative treatment of the subject by a veteran writer. Not only are the paleontological findings recorded and summarized, but philosophical discussions on evolutionary relationships are presented. While the evidences used are obtained chiefly from the rocks, the morphology of existing plants has not been ignored.

The Origin of a Land Flora.—By F. O. Bower, University of Glasgow. First edition, 1908, 727 pages and 261 illustrations; Macmillan & Company, Ltd., London. The author here presents an hypothesis concerning the origin of the higher plants and the part played by the presence of land above the waters that had long covered it. In presenting his evidences the author has assembled data of much value aside from their bearing on the topic of the book.

Primitive Land Plants.—By F. O. Bower, University of Glasgow. First edition, 1935, 658 pages with 465 illustrations; Macmillan & Company, Ltd. This book is not a revision of "The Origin of a Land Flora" by the same author, but in a somewhat different way the same subject matter is presented, with the

added information gained in nearly 30 years of research by many investigators.

The Evolution of the Land Plants.—By Douglas Houghton Campbell. First edition, 1940, 731 pages, 351 illustrations; Stanford University Press. The book presents a critical discussion of phylogenetic relationships among the higher categories of bryophytes, pteridophytes, and spermatophytes, based not only on paleobotany but bringing in morphological studies of living plants and other lines of evidence.

Plant Life through the Ages.—By Albert C. Seward. Second edition, 1933, 603 pages, illustrated with nine reconstructions of ancient landscapes; The Macmillan Company. A geological and botanical retrospect, not too technical for general use.

Paleobotany: A Sketch of the Origin and Evolution of Floras.—By Edward W. Berry, Johns Hopkins University, *Ann. Rpt. Smithsn. Inst.* 1918, 119 pages and 42 illustrations. A concise account, suitable to the needs of botanical students, summarizing our knowledge of fossil plants, especially the pteridophytes and spermatophytes. Valuable diagrams are given on the prevalence of different groups during past epochs.

Plants of the Past; a Popular Account of Fossil Plants.—By Frank H. Knowlton, U. S. Geological Survey. First edition, 1927, 275 pages and 90 illustrations; Princeton University Press. This book, from an authoritative source, gives the general reader a clear idea of plants that have existed on the earth at different geological periods and the reasons for changes in flora. It also has chapters on the importance of plants to prehistoric animals and on coal production.

Tree Ancestors.—By Edward W. Berry, John Hopkins University. First edition, 1923, 270 pages and 48 illustrations and maps; The Williams & Wilkins Company. A discussion of the past and present status of some of the most important families of woody plants, presenting valuable information in a most readable style. The book gives clear-cut explanations of the peculiar distribution of many species, the survivors in favored localities of once cosmopolitan races.

INDEXES, CATALOGUES, ETC.

From time to time works have been written summarizing the advancement that has been made in the study of plants. These

are of especial value in locating the literature on different phases of the subject.

Thesaurus Literaturae Botanicae.—By G. A. Pritzel, Berlin. Second edition, 1872, 254 pages, unillustrated; F. A. Brockhaus, Leipzig. The chief botanical publications up to 1872 are listed under the names of the authors, arranged alphabetically, and in a later section classified by subjects. About 15,000 references are given.

Genera Siphonogamarum.—By C. G. de Dalla Torre and H. Harms, Berlin. First edition, 1900–1907, 921 pages unillustrated. This is a valuable aid in the tracing of generic synonymy. Following a list of families of spermatophytes some 637 pages are devoted to lists of genera, arranged by families and subfamilies, and showing the sections of the genera, if such occur. The synonymous names of genera and sections are given, with dates and citations. The last part of the book is taken up by a huge index of 284 pages containing all the generic and sectional names used in the text. The work follows the Engler system.

Index Kewensis Plantarum Phanerogarum.—By B. D. Jackson, Kew Herbarium, under the direction of Jos. D. Hooker. The original work (1893–1895) consisted of four large volumes having a total of 2,567 pages, unillustrated, and to these have been added nine large supplements; Oxford University Press. This monumental work lists all species described since 1753 under their genera, which are arranged alphabetically, and each specific name is accompanied by a reference to the original publication. Nonvalid synonyms are in italics and referred to the accepted name. It is indispensable to the research worker in taxonomy of flowering plants.

Bradley Bibliography.—By Alfred Rehder. Five volumes. Publication No. 3 of the Arnold Arboretum; Riverside Press, 1911–1918. A guide to the literature of the woody plants of the world that were described before the beginning of the twentieth century.

Index Londinensis to Illustrations of Flowering Plants, Ferns, and Fern Allies.—By Otto Stapf and O. C. Worsdell. A six-volume set published by the Oxford University Press. Edited by Stapf up to 1921, with a two-volume supplement by Worsdell from that date to 1935. It is an amended and enlarged edition of Prezel's "Alphabetical Register" continued to a later date.

The Gray Herbarium Card Index.—By the Staff of the Gray Herbarium. A set of cards listing all new names and new combinations for genera, species, varieties, and forms of flowering plants, ferns, and fern allies of the Western Hemisphere. Issued quarterly to subscribers. About 258,000 cards have been published to date. It is invaluable for research work in plant taxonomy.

North American Flora.—Published by the New York Botanical Garden, from 1906 to date. Thirty-four volumes were published up to 1940. This great work is intended to furnish descriptions of all the wild plants of North America.

MISCELLANEOUS

The simple grouping used in this chapter for the literature of systematic botany leaves some important publications unclassified.

A Glossary of Botanical Terms.—By B. D. Jackson, Linnaean Society of London. Seventh edition, 1928, 481 pages, unillustrated; J. B. Lippincott Company. Most manuals include glossaries of the terms used, and in most circumstances these are sufficient for the purpose intended. Many technical terms used in botanical science are not, however, included in these limited lists. Furthermore, some terms require a fuller discussion than space will permit in connection with a crowded manual. This book fills the needs just indicated in an admirable way.

Glossary of Botanical Terms Commonly Used in Range Research.—By W. A. Dayton, U.S. Department of Agriculture Miscellaneous Publication No. 110, 40 pages, illustrated. While this pamphlet is intended primarily for use in forestry work, it is very suitable and convenient for students in systematic botany.

Outlines of the History of Botany.—By R. J. Harvey-Gibson, University of Liverpool. First edition, 1919, 274 pages, unillustrated; A. & C. Black, Ltd., London, and The Macmillan Company. A well-balanced discussion of the development of botanical science, including especially its taxonomic, morphological, and physiological aspects. It is authoritative, unprejudiced, and executed in a style well suited to student use.

Native American Forage Plants.—By Arthur W. Sampson, University of California. First edition, 1924, 435 pages and 200 illustrations; John Wiley & Sons, Inc. The subject is treated

with especial reference to the Rocky Mountain and Pacific regions but applies in a measure to the entire country. The treatment is particularly effective and convenient. The plants are grouped by families, and the more important species are clearly described. Valuable information is given concerning their distribution, abundance, palatability, and nutritive value. Summary tables facilitate the finding of desired information.

Useful Wild Plants of the United States and Canada.—By Charles F. Saunders. First edition, 1920, 275 pages and 74 illustrations; Robert M. McBride & Company, New York. This book is written in semipopular style, using both common and botanical names. It summarizes our knowledge of the past and present use of plants by the Indians and the white men that followed them. In addition to assembling the knowledge acquired by others, the author adds many of his own observations. Special emphasis is laid on the use of plants for food, but medicinal and other properties are considered also.

Manual of Weeds.—By Ada Georgia, Cornell University. First edition, 1914, reprinted in 1940, 593 pages and 386 illustrations; The Macmillan Company. Following a chapter on the fundamental principles of weed development, dissemination, and control, several hundred weed species are described and discussed. The arrangement is by families, and both common and botanical names are given. Under each species are given the source, means of propagation, season of development, distribution, and habitat. The methods of control are briefly indicated.

Taxonomy of the Flowering Plants.—By Arthur M. Johnson, University of California at Los Angeles. First edition, 1931, 864 pages and 478 original illustrations; D. Appleton-Century Company, Inc. This book is written as an aid to teachers and students of taxonomy. Part I is chiefly concerned with morphology in its relation to taxonomy. Part II is a description of groups of angiosperms. No pretense is made of describing every species, and more space is therefore available for the species and larger groups that merit special attention. In general the Engler and Prantl system is followed.

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Numbers in **bold-face** indicate pages bearing illustrations. Generic and specific names are in *italics*.

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